

Predicting salmonid population ecology from individual  
fish responses to environmental changes: bridging  
behaviour, conservation and fisheries management

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Predicting salmonid population ecology from individual fish responses to environmental changes: bridging the gap between behaviour, conservation and fisheries management. – Phang, S.C.

## **Abstract**

Current habitat-association models used in the management of the socio-economically and ecologically important chalk stream salmonid populations fail to incorporate fish behaviour and the interactions between fish with their environment and this limits their ability predicting management-relevant salmonid population responses to environmental change. A salmonid individual-based model is parameterised to predict fish distributions and growth as the modelling approach address the weaknesses of current models. Virtual forager parameters are derived from published investigations and models of salmonid behaviour and bioenergetics. Data from three field studies at the same chalk stream site are used to describe the environment and initial fish population with subsequent data on fish population patterns used to statistically validate the IBM. I found that current recommendations for population enhancement may be futile beyond a threshold population density and regimes that address habitat quality should be adopted. Potential parasite impacts are investigated theoretically by simulations on the mode of impact on their host and identify the most population damaging parasites as those with high effect on host physiology. The management of salmonid predators in fisheries is predicted to have little benefit to salmonid growth and should not be implemented. Additionally, the removal of the dominant aquatic macrophyte for flood risk management is potentially damaging to salmonid populations and recommendations for a sympathetic design are provided. The model described here can be used to produce robust predictions of salmonid population patterns in riverine habitat and allows users to test the impact of environmental change on salmonids to be used for proactive management in light of current rates of environmental change.

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### **Author’s declaration**

I confirm that the work presented in this thesis is my own work, with the following exceptions:

The 2008 dataset on Mill Stream environment and fish population is owned by Bournemouth University and was collected under the Marie Curie 2008 PRIME project. Access to this dataset was part of this PhD project.



# **Chapter 1. The importance of salmonid fish, the challenges faced in their management and the potential of individual-based models to address them**

## **1.1 Introduction**

The challenge for environmental managers is account for multiple ecological processes and synthesise all relevant theories into their management. The impetus for such an approach is high but the tools to achieve this still need to mature. Proactive, evidence-based management requires science to develop itself to understand the relationships of dynamic, multi-scale interactions and build better predictive models to ensure the sustainable viability of natural resources.

Among all ecosystems worldwide, freshwater ecosystems represent an increasing strategic issue linked to the allocation of water as a natural resource shared among several ecosystem services such as agriculture, fisheries, leisure and domestic consumption (Costanza et al. 1997; Gozlan & Britton 2013; Kuylensstierna et al. 1997). The resource is ecologically, socially and economically important and thus the scale and variation in stakeholder interests poses a demanding and complex management landscape (Vorosmarty et al. 2010; Dudgeon et al. 2006; Gozlan & Britton 2013). In light of overexploitation, environmental change and species introductions, freshwater fisheries are a freshwater ecosystem service that faces an uncertain future (Vorosmarty et al. 2010).

The general trend is for fisheries management to move from ‘single-species’ to an ‘ecosystem approach’ (FAO 2012). Historically, fishery models have either been population-centric (e.g. stock size and limits) or with a more recent appreciation for the importance of the environment and potential population size (e.g. HABSCORE). The limitation of these approaches is they consider effects in isolation; population models do not account for environmental changes whilst habitat models disregard characteristics of the

species and population (Grimm & Railsback 2005). Furthermore, whilst management is concerned at the scale of the population, potentially important interactions and behaviour of the individuals that comprise the population are often overlooked by both typical population and habitat models (Grimm & Railsback 2005).

Scientists are developing new tools to model the multiple and complex interactions in an ecosystem. These tools provide a more realistic representation of the natural systems and will help achieve an ecosystem-approach to management. One mechanistic modelling approach that is able to do this is individual-based modelling where the interactions (and resulting consequences of these interactions) of individuals within a population and with the environment are modelled through computer simulations (Grimm & Railsback 2005; Stillman 2008). Individual-based models are able to tackle the problem of assimilating current knowledge of the 'simple' parts of a freshwater system by collating research at all scales (Grimm & Railsback 2012). However, an inevitable consequence is that they are more complex than traditional models and thus there may be initial hesitancy in their uptake. Scientists need to meet this challenge through clear and thorough assessments of models to validate predictions. In part, this is being addressed through the development of specific methods for building, testing and communicating these types of models (Grimm et al. 2006).

The aim of this research project is to develop an individual-based model specifically for salmonid fishery management by linking and incorporating current scientific understanding of different aspects of salmonid biology and behaviour within a virtualised environment. The first task is to robustly test the designed model structure and its assumptions before taking advantage of the predictive power and utility of the IBM approach by addressing specific information-gaps for management decisions.

## 1.2 The value of freshwater resources and fisheries

Natural resources are economically important and essential in terms of ecosystem provision such as clean air, water and food among others (Foley et al. 2005; Pauly et al. 2002; Gozlan & Britton 2013) that greatly contribute towards our standard of living (Costanza et al. 1997). These ecosystem services provide a multitude of numeral abiotic and biotic exploitable resources that underpin economic, cultural, aesthetic, scientific and education markets (Dudgeon et al. 2006).

From an ecological perspective, freshwater systems are an important habitat for a high biodiversity of fish, invertebrate and plant species (Lundberg et al. 2000, Strayer 2006, Chambers et al. 2008). Whilst only comprising an area of 0.8% of the total earth's surface, they support nearly 6% of all described species making them a disproportionately conspicuous source of biodiversity (Dudgeon et al. 2006). Across the globe, changes to the environment are leading to a significant impact to ecological systems (Walther et al. 2002) and freshwater systems are not immune to this threat. Furthermore, there is growing concern over the future global accessibility to water (Kuylenstierna et al. 1997). The demands placed on freshwater systems from an increasingly larger and more demanding human population has led to the degradation in the health of global freshwater systems (Vorosmarty et al. 2010). Processes including, but not limited to, over-exploitation, pollution, modified flow regimes, habitat manipulation, invasive species and climate change have been identified as some of the primary threats to freshwater biodiversity (Dudgeon et al. 2006; Gozlan et al. 2005, Hogg & Norris 1991; Pinder et al. 2005; Strayer & Dudgeon 2010; Xenopoulos et al. 2005). As restoration efforts of degraded habitats are typically costly and with no guarantee of positive results, there is a drive for freshwater management to shift towards a predictive and preventive approach as opposed to being historically intuitive and reactive.

Among all freshwater ecosystem services, fisheries serve as a daily source of protein for millions of people and are thus particularly strategic with increasing pressure to become sustainable. With an estimated annual harvest of 14 million tonnes, freshwater fisheries employ nearly twice as many fishermen as those at sea (i.e. 20.7 million against 12.4 million respectively), with up to 60 million people in the developing world dependent on river fisheries for their livelihoods and millions more relying on them for food, there is a tremendous social benefit to a sustainable management system (Gozlan & Britton 2013). There is great impetus to safeguard the future of these systems and the resources they provide. In developed countries fisheries may serve a different fishing role with fishing seen primarily as a sporting or leisure activity, nonetheless, the economic values generated by these industries are high (Holmlund & Manner 1999; Arlinghaus, et al. 2002). On average, it is estimated that in countries with reliable statistics,  $10.6\% \pm 6.1$  (mean  $\pm$  S.D.) of the total population participate in recreational fishing (Arlinghaus & Cooke 2009). In the United Kingdom, recreational fishing is an industry with both high social and economic value and with an estimated 4 million regular anglers that generates an estimated UK£ 3 billion annually (Environment Agency 2004).

As the social frameworks of recreational fishing compared to fisheries for food are fundamentally different, so are the management options of these fisheries (Food and Agriculture Organisation 2012). Recreational anglers see their fisheries as leisure and whilst a few fish may be taken for consumption, their main concern is with fishing access and the production of large specimen fish and may pursue the introduction of species with good sporting qualities (Walters & Kitchell 2001). As such, recreational fisheries managers are prone to implement potentially ecologically destructive and unsustainable practices like introduction of non-native species and environment manipulation to favour specific game fish species (Lewin et al. 2006). It is then important for recreational fishery management to look

towards an aquatic stewardship and consider the overall impacts to freshwater ecosystem (FAO 2012).

Game fishing in the UK is typically composed of either coarse or game (predominately salmonid species like brown trout, *Salmo trutta* and Atlantic salmon, *Salmo salar*) fishing. Of the estimated 30 million days fished in 2005 by registered fishers in the UK, 88% of the time was spent coarse fishing and the remaining on game fishing (Mawle & Peirson 2009). However, the economic value of game fishing is high as the total cost spent per average game fishing trip (£175) is nearly six times the average expenditure spent on a coarse fishing trip (£36) (Mawle & Peirson 2009). Game fishing typically comprises of fishing on stocked brown trout fisheries in lakes and other watercourses or privately owned wild fisheries on salmonid rivers. These wild fisheries represent an economically valuable asset as it drives ‘fishing tourism’ where fishers travel outside of their region to fish them (EA 2004). Consequently, the value of salmonid fishing varies per region based on the location of salmonid rivers. In southwest England, chalk streams are enigmatic salmonid rivers and support resident wild populations of Atlantic salmon and brown trout. Game fishing for salmonids constitutes more to the regional fishing industry (24%) than the national average (18%) (Mawle & Peirson 2009). However these fisheries are not immune to the global trend of declining wild salmonid populations; returning numbers of adult Atlantic salmon in one chalk stream, the River Frome, is currently at 30% of pre-1980 numbers (Game and Wildlife Conservation Trust, *unpublished data*). It is important that this decline is halted and reversed to ensure the long-term future of an ecologically and economically important resource.

### 1.3 The chalk stream environment and its ecology

Chalk streams are recognised by their distinct geological and ecological characteristics. Berrie (1992) describes that the key property giving chalk streams many of its characteristics is the calcareous geology they are found on. The porous geology facilitates relatively quick infiltration of precipitation into the water table and chalk streams are predominantly fed from ground water springs as opposed to surface runoff. This process filters out particulates in the water and chalk streams are usually clear with low turbidity. Absorption into the chalk aquifer also delays the time it takes for water to enter the chalk stream (long lag phase) resulting in relatively stable discharge and temperature regimes. Groundwater levels are typically recharged during the higher precipitation winter periods and feed the chalk streams during the drier summer periods.

The clear waters of chalk streams facilitate high rates of primary productivity (Edwards & Owens 1960), which in turn supports a high density of invertebrates and fishes. Water crowfoot (*Ranunculus spp.*) is the dominant in-stream aquatic macrophyte and can grow sufficiently to affect local hydrology and channel characteristics (Dawson 1989). During the summer months from April till October, it grows into large plume-like structures that affect the flow of water around it (Dawson 1989). Hydrodynamic shelters comprising of low flow velocities around the plant structure are utilised by fish and invertebrates as velocity refuges (Harrod 1964). The physical structure of the plant also provides cover from both terrestrial and aquatic predators (Savino & Stein 1989).

Chalk streams have high aquatic invertebrate biodiversity and densities in excess of 170,000 inverts.m<sup>-2</sup> (Wright & Symes 1999). These invertebrates typically inhabit structural habitats either in or on riverbed substrate and aquatic vegetation. A percentage of these invertebrates, either on purpose (dispersal behaviour) or dislodged by water currents, will enter the water

column as ‘drift’ (Brittain & Eikeland 1988). Invertebrate drift displays a spatial and temporal distribution; habitat characteristics dictate the immediate invertebrate community and density and there is a strong diel pattern with increased drift at dawn and dusk as these are the times invertebrates found on substrate or macrophytes will purposefully enter the water column (Brittain & Eikeland 1988). Drifting invertebrates represent a rich food source for fish and with clear and relatively warm water temperatures, chalk streams an ideal habitat for salmonids.

Salmonids are ‘drift feeders’ and feed on invertebrate drift by swimming at a speed equal to channel velocity and wait for drifting invertebrates to enter a ‘capture window’ and upon detection the fish will actively swim towards the prey item to capture it before returning to its original station (Hughes et al. 2003). Each capture attempt represents an energetic cost that can be estimated by calculating the bioenergetic costs of swimming distance and swimming speed (Hayes et al. 2000; Hughes et al. 2003; Piccolo et al. 2008a). At higher velocities, the probability of a successful capture decreases (Piccolo et al. 2008b). For fish bioenergetics, the size structure of the invertebrate drift is important as whilst each feeding event (i.e. the capture of a single item) for a drift feeding fish may represent a similar bioenergetic cost of capture, the nutritional value provided is dependent on the size of the invertebrate (Benke et al. 1999). The minimum and maximum size of invertebrate that can be consumed by a fish is determined by the space between gill rakers (Wankowski 1979).

The amount of invertebrate drift entering the capture window of a fish is dependent on a multitude of factors including water velocity and the density of drifting invertebrates (Hayes et al. 2000) and the location feeding fish occupies are important parameters affecting the rate of consumption of a fish. Salmonids display territorial behaviour over the best locations within the river and dominance between conspecifics is ranked on the fish size with dominance decided by size (Johnsson et al. 1999). The area of territory

defended has a positive relationship with fish size and larger fish need to defend a larger area to feed to fulfil their higher bioenergetic requirements (Elliott 1976a; Imre et al. 2004; Dill 1978). Salmonid population density and territory size have been used to estimate a site's carrying capacity (Grant & Kramer 1990).

Apart from brown trout and Atlantic salmon, chalk streams also support dace (*Leuciscus leuciscus*), roach (*Rutilus rutilus*), stone loach (*Barbatula barbatula*), European eel (*anguilus anguilus*) and bullhead (*Cottus gobio*) (Berrie 1992). The predominant aquatic predator in the chalk stream ecosystem is the European pike (*Esox lucius*) and it is a predator of nearly all other chalk stream fishes, including salmonids, and smaller pike (Mann 1982).

The River Frome is one such chalk stream system and is located in the Dorset County in southern England. The catchment land use is primarily agricultural or managed for livestock but the river remains relatively pristine. Sections of the river have been designated as Sites of Special Scientific Interest (SSSI), a merit awarded by Natural England and is a legislative designation conferring particular standards of environmental quality and legal protection (Natural England 2012). The majority of the river is managed as private fisheries and there is very limited public access. Chalk stream fisheries are a lucrative and locally important trade. Local communities reap the benefit of healthy fisheries through the generation of income by the purchasing of fishing licenses and being patrons of local hospitality services. Consequently, the health of fish populations within these chalk streams are of high socioeconomic importance.



## 1.4 Threats to and the management of chalk streams

### 1.4.1 Overview

In the River Frome, Atlantic salmon populations have experienced a steep decline with the number of adult salmon currently returning to spawn a third of pre-1980 numbers (Game and Wildlife Conservation Trust *unpublished data*). The anadromous behaviour of salmon and sea trout (a small proportion of brown trout migrate to the sea to feed) means there is a premium placed on the management of freshwater habitats for salmonid conservation given the difficulty in managing the scale of marine habitats (Gibson 1993). However, stakeholder interest and involvement in freshwater habitats are diverse and conflicts exist (Dudgeon et al. 2006). Freshwater habitats are not managed solely for the benefit of salmonid populations and efforts must be made to ensure to assess the effects of both fishing and non-fishing management regimes on salmonid populations. In chalk streams, two widely employed management regimes are the cutting of dominant aquatic macrophyte (*Ranunculus spp.*) to reduce potential flooding and the culling of European pike to reduce predation rates. There is a need to identify the extent these management schemes are affecting freshwater salmonid populations.

### 1.4.2 In-stream weed management

*Ranunculus spp.* is the enigmatic, dominant aquatic macrophyte in chalk stream habitats. It grows quickly in the warm and bright spring and summer months but can grow thick and widespread if unmanaged affecting local hydrology by increasing flow resistance, which leads to significantly reduced channel velocity and an increase river depth by as much as 0.7m (Bal & Meire 2007; Dawson 1989). As water retention times increase, groundwater levels rise and coupled with reduced drainage capacity due to dense macrophyte growth, there is an increased risk of flooding if there is high summer rainfall. Consequently, the Environment Agency (EA) will implement cutting regimes to reduce the biomass of *Ranunculus spp.* to

reduce the risk of flooding (Dawson 1989). Additionally, fishery management may cut in-stream macrophytes to reduce the extent of thick aquatic macrophyte growth to increase the fishing access of a stretch.

The timing that the macrophyte is cut is important to achieve reduced biomass (Dawson 1989; Bal & Meire 2007). Under natural conditions, *Ranunculus spp.* grows into large dense structures and flowers in early summer and then begins a slow die back in late summer to leave rhizomes and roots as it overwinters (Dawson 1989). Under a typical management regime, stands of *Ranunculus spp.* will be subject to two cutting events, the first in spring and the other in late summer (Dawson 1989). The spring cut results in a short-term reduction in biomass but high compensatory growth may actually result in a stand biomass at the end of summer similar to if there was no management and a second cut in late summer is often required (Dawson 1989). Dawson (1989) also showed that after a four-year period of no cutting, the biomass of *Ranunculus spp.* stands may be below that if a cutting regime was implemented, but the risk of summer flooding would still exist, as the stands of *Ranunculus spp.* still remain.

The removal of *Ranunculus spp.* will result in a significant environment perturbation of the chalk stream ecosystem. Changes in water velocity, distribution of shelter and invertebrate drift densities are all likely to affect salmonid and fish populations as bioenergetics are impacted. Understanding the type and extent of impacts to changes brought about by aquatic macrophyte management is important as it assesses flood risk management regimes holistically, referencing impacts on the locally important fishing industry; the design of salmonid-sympathetic *Ranunculus spp.* removal should be pursued.

#### *1.4.3 Predator control*

European pike (*Esox lucius*) are the dominant piscivorous fish in chalk streams and will predate salmonids (Mann 1982). Fishery managers

implement pike culling regimes to reduce predator impacts on angler targeted salmonid populations (Mann 1989). The removal of predators will remove population loss by predation and will also alter time budgets of fish; prey fish dedicate less time and energy to antipredator behaviours (Jackson & Brown 2011; Vilhunen & Hirvonen 2003). Antipredator behaviours increase survival from predators but as non-feeding behaviours, the overall growth may be impacted (Dannevit & Petersson 2001). However, management needs to consider the potential for predator-culling regimes to cause erratic patterns in prey populations (Estes et al. 2011; Chapin 2000). Predators perform ecologically important functions of removing weak or diseased individuals, which results in increased population health (Thorp 1986). Furthermore, the removal of pike contradicts to the currently lauded, ecosystem-approach to freshwater management (Francis et al. 2007).

Management must also consider the manually intensive and repeated nature a regime of pike culling entails (Mann 1989). The most common method of pike removal involves labour-intensive electric fishing and the method is not completely efficient and some pike will escape capture. A site will also be repopulated from the immigration of pike from other areas in a ‘source-sink’ movement or spawning from missed pike. However the greatest reason against pike removal is the simultaneous removal of the self-regulating process of cannibalism. The removal of large pike often leads to an increase in the number of small pike, which in time will grow and repopulate (Mann 1989). Furthermore increased densities of small pike alter predation pressure on small salmonids which may affect long-term salmonid population dynamics (Mann 1989).

Given these complexities, the practice of pike culling is increasingly scrutinised for its relevancy in modern fishery management. An investigation by the Game and Wildlife Conservation Trust (GWCT) on salmonids numbers during a period of pike removal and subsequent cessation of the practice found a non-significant difference in salmonids numbers, except for large adult trout which were found in lower numbers

(Game and Wildlife Conservation Trust unpublished data). However, the pike that were present were too small to be predators of large trout and hence could not cause this reduction. Natural population fluctuation and possible predation by other non-pike predators (e.g. avian predators) are cited as possible reasons (Game and Wildlife Conservation Trust personal comm.). These results contradict traditional assumptions of positive impacts associated with pike removal and so fishery management must review the relevancy of the regime in current and future policies. The uncertainty surrounding the effects (positive or negative) of the practice needs to be clarified. Alternatively, if data does support the management practice, can the management practice be modified to incorporate the ecological benefits associated with predation and balance both the wants of the anglers and overall ecosystem health?

#### *1.4.4 Population manipulation by enhancement practices*

Traditional fishery management often prioritises the benefit of angler-targeted fish species (Francis et al. 2007) leading to management regimes aimed at increasing the populations of these fish (Walters & Kitchell 2001); in chalk streams, management regimes often prioritise salmonid species. Gravel cleaning involves the removal of fine sediment from riverbed substrate and improves the flow of water and oxygen through it (Meyer et al. 2008). Salmonid eggs laid in cleaner gravel have higher rates of survival and should lead to greater number of fish recruited (Heywood & Walling 2007). Management may also seek to increase population densities artificially by stocking fish that have been hatched and reared elsewhere into the chalk stream ecosystem. However stocked fish can pose a potential negative impact to resident wild stocks through genetic dilution and increased competition (Hansen 2002; Deverill et al. 1999). Stocked fish from aquaculture are recognized to have lower competitive and breeding ability that similarly sized wild conspecifics (Milot et al. 2013) and a population consisting of a high proportion of stocked fish may have less

long-term sustainability than a smaller population of wild fish (Krueger & May 1991).

Changing the population density in a site may only be relevant if the site can sustain more numbers of fish (i.e. current densities are below carrying capacity). Regimes of population enhancement should only be pursued if the habitat can sustain the increase otherwise the regime would not achieve increased population densities and would represent an inefficient use of resources. Management should identify which sites are more appropriate for population enhancement regimes or should look to implement regimes that increase the habitat quality so that more fish can be supported. A tool that is able to predict the impacts of increasing populations on local populations would be of great benefit for management, as it will help prioritise decision-making leading to efficient resource use.

#### *1.4.5 Parasite introduction*

An increase in the global movement of fish and other aquatic material has led to the introduction of non-native species to freshwater habitats and they pose a threat to local biodiversity (Dudgeon et al. 2006). In particular, the introduction of non-native parasites can have a significant negative impact on health of both the host population and the community at the point of invasion (Gozlan et al. 2005; Okamura & Feist 2011). Management needs to be proactive in their decision-making and response to this threat with the aim to prevent the initial introduction because intervention may be ineffective after the parasite has introduced and established itself (McCallum & Dobson 1995). The identification of problem parasites prior to their introduction would be of great assistance in designing management appropriate, preventative management regimes (Manchester & Bullock 2000).

It is difficult to plan a targeted and preventive regime without being able to predict the movement and successful introduction of non-native parasites

(Whitney & Gabler 2008). One way to help management to prioritise resources in dealing with this threat is prioritise the potential threat different parasites might have when introduced. Following this, resources can be diverted to investigate the viability of an introduction and the design of relevant regimes. Given the high biodiversity in parasites (Poulin & Morand 2000), it would be a significant task to predict impacts for each parasite and an approach where the type of parasite impact (as opposed to the impacts of a specific parasite) is instead investigated instead may prove a useful step. A better understanding of the parasite threat and introduction will help in establishing parasite risk in salmonid management.

## 1.5 Predictive modelling and its potential in ecological management

Managers of freshwater systems face a challenging task as they have to contend with environmental changes at both the local, regional and global scales, assess multiple input stressors and meet the needs of diverse stakeholder groups whilst also ensuring management decisions are dynamic and as informed as possible (Rogers 2006). Decisions need to be based on robust evidence but it is a challenge to collecting and interpreting appropriate information. Experiments and/or observations are one potential source but the relevancy and applicability of findings may reduce the reliability in the conclusions drawn. The difficulty of an experimental approach lies in, amongst others, the impracticalities of time, the identification of suitable sites and replicability (Carpenter et al. 1995). Additionally, the findings of experimental results will also be limited in their applicability beyond similar environmental and population characteristics which may lead to doubts over its utility and relevancy; an increasingly likely scenario in light of novel environmental conditions arising through environmental change. Findings of ecological studies may change even if the same study was performed at the same site if the site has

undergone environmental change (Maddock 1999). The appropriateness of an experimental approach will be challenged when investigating scenarios that have the potentially serious negative effects such as the introduction of disease and non-native species; alternative approaches that can produce robust and workable ecological solutions are thus a premium.

One potentially powerful tool available to help guide freshwater biodiversity management is the use of predictive ecological models (Sutherland & Freckleton 2012). These models vary in complexity and can impart information from theoretical to applied. Analytical models of population dynamics like the logistic and Lotka-Volterra equations have added much to our theoretical understanding of population interactions as whilst they respectively predict the effect of density dependence and predators on the dynamics of a single population, they do not consider the environment and this limits their use in applied scenarios (Grimm & Railsback 2005). Though these equations are theoretically important, they are not sufficient in their predictions to influence predictive management (Grimm & Railsback 2012). Another commonly used model in management are habitat assessment models (e.g. HABSCORE & PHABISM) and these do account for habitat variables in their predictions (Milner et al. 1998; Maddock 1999). However, despite some success, habitat assessment models are derived from empirical observations of population abundance and habitat quality which means that their predictions are limited to the distribution of habitat parameters and population densities the relationship was parameterised from and so their applicability in new habitats often is not ensured (Guisan & Zimmermann 2000). Furthermore habitat assessment models focus in on the environment and do not consider the potential adaptive responses by individuals in the population to changes in habitat quality (Guisan & Zimmermann 2000). Loreau (2010) describes the potential benefits of linking all ecological disciplines, from species traits upwards to ecosystem functioning in a unifying ecological theory.

An important aspect in a population's ability to respond to an environmental change is the behavioural adaptability at the level of the individual (Caro 2007). Populations consist of individuals and how these individuals can respond to changes in their environment can determine how the population copes with impacts linked with environmental change (Sih et al. 2004; Walther et al. 2002). Despite a strong acknowledgement to the contribution behavioural insights can add to conservation efforts, its full potential has not been realised (Caro 2007). Traditional conservation management has often omitted this potentially important aspect due to the complexity of scales; how do individual responses contribute to, conservation-relevant, population patterns and of the several behaviours, which of these are relevant to the conservation issue. Though challenging, the potential contribution to conservation is high and incorporating behaviour into management decisions is an avenue that should be pursued (Caro 2007).

Caro (2007) suggests that one reason causing the poor integration of animal behaviour into conservation biology is the lack of an established method for bridging the two. One such approach that has had success in producing predictive ecological models that are able to link individual interactions with population level effects are 'Individual-Based Models' (IBM) (Judson 1994; Grimm & Railsback 2005; Stillman et al. 2001). Within an IBM, individuals are considered discrete entities and during a simulation, there are interactions between individuals with each other as well as between individuals and their environment. Individuals display 'adaptive behaviours' which are behavioural decisions derived from both the environmental conditions and the individual's traits to seek the option that returns the highest fitness for the individual. For example, a large fish might make a different decision than a smaller conspecific even faced with the same environmental conditions because their individual traits differ (e.g. bioenergetic demands). IBMs have increased in their popularity due to greater accessibility because of increased computational power that can simulate the high number of individual interactions within a population.



Individual-based ecology and individual-based models are underpinned by the theory that the patterns observed occurring at the scale of the population actually arise from interactions and decisions made at the level of the individual (Judson 1994, Grimm & Railsback 2005). Thus, by modelling the processes and decisions of multiple individuals, patterns at higher scales will emerge through the interactions between individuals and with their environment (Grimm & Railsback 2005). Whilst the scale of prediction is the same, this is a shift from population centric to a focus on individuals and their interactions; individuals adapt and respond to each other and their environment and an IBM model will therefore be a more realistic representation of reality than classic population models. Uchmanski & Grimm (1996) define four important aspects that make up an IBM and these are 1) lifecycle change in individuals or growth; 2) resources used by individuals; 3) real and whole individuals and 4) some variability between individuals. Models that do not meet this criterion should be referred to as ‘individual-orientated’ (Grimm & Railsback 2005). IBMs have had demonstrable success as applied predictive ecological models and several notable applied examples include but are not limited to: Individual-based Stream Trout Research and Environmental Assessment Model (inSTREAM) for brown trout in North America, MORPH for shore birds along the UK coast and wood mouse populations (see Railsback et al. 2009; Stillman & Goss-Custard 2010 and Liu et al. 2013 respectively).

Depending on the type and number of behaviours or interactions modelled, IBM complexity can range from simple to very complex. The challenge for the modeller is to encapsulate all necessary behaviours and parameters to represent what is effectively a complex community or ecosystem (Grimm & Railsback 2005). For clarity, IBM construction should follow a ‘pattern-orientated modelling’ methodology whereby model assumptions are repeatedly validated by comparing whether the patterns predicted by virtual

individuals are in agreement with patterns observed in real populations (Grimm & Railsback 2005).

Given the potential predictive power of IBMs and their proven record of successful application to real ecosystems, an IBM parameterised to model salmonid populations in chalk streams could be an informative tool for management decisions. The inclusion of both environmental and individual parameters in IBMs makes them an ideal modelling candidate for chalk stream management; each stretch (i.e. fishery) within a river will have a slightly different environment and salmonid populations and a salmonid IBM can be parameterised for a specific stretch. An IBM approach also allows parameter manipulation to predict patterns even under novel parameter conditions (Stillman et al. 2000).

## 1.6 Project aims and objectives

The aims of this project are to predict the impacts scenarios of environmental change have on the chalk stream salmonids brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*). The predictions will be quantitative as resulting changes to fish growth rates and their distribution within the system are analysed. Results will be interpreted within the context of management decisions through the identification of threats and possible steps that could minimise potential negative impacts. The objectives are to:

1. Parameterise and calibrate (if necessary) a salmonid-specific IBM that is able to predict the population patterns of salmonid growth and distribution in a stretch of chalk stream and validate these predictions with observed patterns of real fish under the same environmental conditions.
2. To plan and collect empirical measurements of salmonid population patterns and environmental conditions within a chalk stream habitat to parameterise and validate the salmonid IBM.
3. Utilise the IBM's predictive power to predict population pattern impacts of four threats to chalk stream ecosystems.
  - a. Manipulation of salmonid populations through stocking and/or population enhancement practices (e.g. gravel cleaning for increased egg survival)
  - b. Identifying and prioritising the threat the introduction of non-native diseases might have on salmonid growth rates
  - c. Investigate the impacts the removal of the main aquatic macrophyte will have on salmonid populations
  - d. Incorporate predator-prey interactions (i.e. antipredator behaviour) to understand the role European pike have on salmonid populations in chalk streams

## 1.7 References

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## 2. Description of field site, fieldwork methodology and environmental datasets

### 2.1 Description of field site

The study site is a side channel of the River Frome in Dorset, south England called the Mill Stream (Dorset, U.K.; 50° 40' 44" N; 2° 10' 42" W) (Figure 2.1). The study site is 520m in length with a width of  $6.25 \pm 0.19$ m (mean  $\pm$  S.E.) and consists of semi-natural chalk stream habitat. The site is heterogeneous habitat with riffles and pools and at the top of the site is a small weir (<50 cm) used to measure Mill Stream discharge by the Environment Agency (NRFA Reference 44001). The Mill Stream channel extends past the bottom of the study site (circa 200m) before re-joining the main channel (Figure 2.2). Fish species found in the site include Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), dace (*Leuciscus leuciscus*), roach (*Rutilus rutilus*), European pike (*Esox lucius*), bullhead (*Cottus gobio*), minnow (*Phoxinus phoxinus*), stone loach (*Barbatula barbatula*) and gudgeon (*Gobio gobio*). Fish populations and movement into and out of the study site was not restricted except for the field investigation carried performed in 2011.

Several sections of the River Frome including the Mill Stream are designated a Site of Special Scientific Interest (SSSI), and there is very limited public access to both the surrounding land (agriculture and livestock) and river. There is some associated game fishing but this is mainly confined to the main channel of the River Frome. Bankside vegetation consists of tree species growing on the south bank that restricts light in some areas. In the sections where there are no bank-side trees present and the dominant aquatic macrophyte (*Ranunculus spp.*) naturally grows in these areas where there is direct sunlight. The land and the river is owned by the Environment Agency and is leased out to research organisations including the Game and Wildlife Conservation Trust based at the local field facility run by the Freshwater Biological Association.

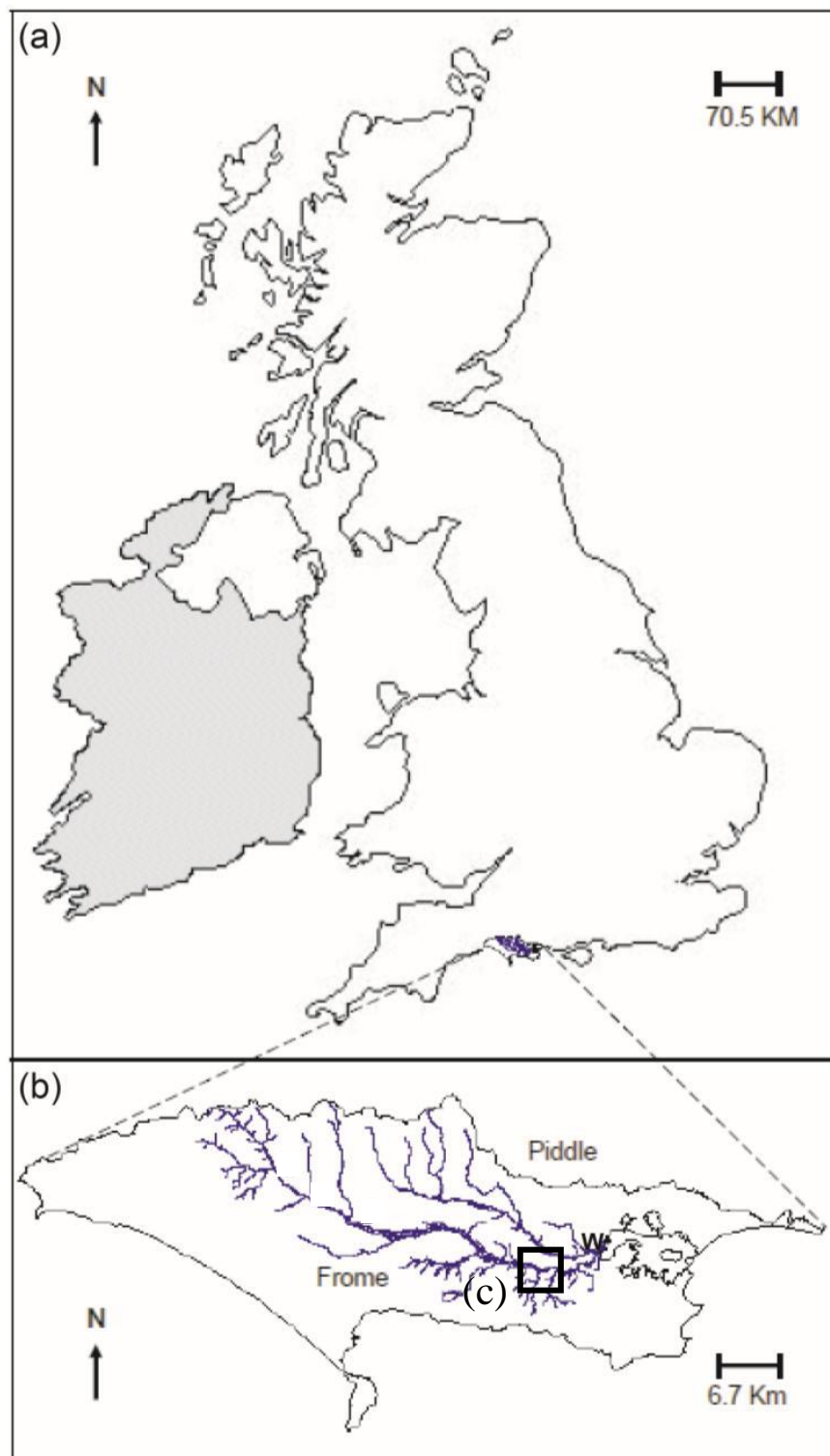


Figure 2.1. The location of the River Frome at the national (a) and regional scale (b). The main study site is a semi-natural side channel of the main river called the 'Mill Stream' (c). Modified from Wood (2012).



Figure 2.2 The Mill Stream (MS – blue line) study site and the main channel of the River Frome (RF) in Dorset, United Kingdom. Significant environmental recording stations are: a discharge station (D) that is managed by the Environment Agency; the fluvarium (F) which controls the amount of discharge entering the study site and a salmon counting station (SC) managed by the Game and Wildlife Conservation Trust, UK.

## 2.2 Field site stretches & patches

To study the distribution of fish within the Mill Stream study site, it is divided into two spatial scales: 1) stretches and 2) patches. A *patch* is an area of homogenous channel habitat ( $59.46\text{m}^2 \pm 21.09$ , mean  $\pm$  S.D.) based on similar environmental characteristics of water velocity, depth, substrate type, aquatic & macrophyte cover and bankside vegetation. Relatively similar patches are grouped into a *stretch* (circa. 80m in length). There are 75 patches and 7 stretches in total (Table 2.1 & Figure 2.3). Numbered wooden stakes were driven into the bank to identify the location of each patch and there was no within channel interference.

Table 2.1 The number and mean area of patches making up each stretch within the study site of the Mill Stream.

Stretch	Number of patches	Mean patch size (m <sup>2</sup> )
1	8	41.07
2	12	37.37
3	11	44.05
4	11	38.42
5	6	48.08
6	8	41.72
7	19	35.08

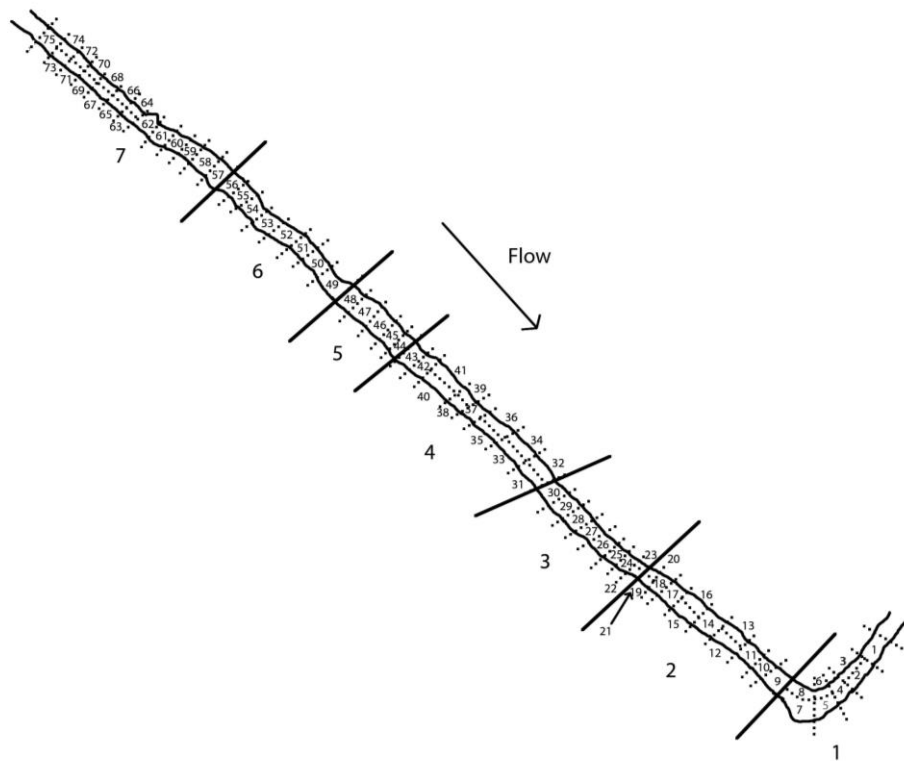


Figure 2.3 The location of stretches (large numbers) and patches (small numbers) used to describe the Mill Stream study site; wooden stakes inserted into the bank helped identify the location of each patch whilst minimising in-channel modification and disturbance.



### *2.3. Description of specialist equipment used*

#### *2.3.1. Passive integrated transponder (PIT) tags*

Passive Integrated Transponder (PIT) tags are programmed with a 16 digit alphanumeric code and this unique sequence identifies specific tags. The code is transmitted when the capacitor within the PIT tag receives electromagnetic power from an external reader. The lack of an inbuilt power source allows PIT tags to be smaller than other commonly used identification tags like radio or acoustic tags (see Hodder et al. 2007). The small size of PIT tags provides utility in tagging small fish for individual identification, which applies specifically to young-of-year salmonids in this investigation. The PIT tags used are either 12.5mm or 23mm half-duplex PIT tags purchased from Oregon RFID Pte. Ltd., USA or 11.5 x 2.1mm full duplex PIT tags purchased from Dorset Identification Pte. Ltd. UK. The difference between full-duplex and half-duplex tag technology relates to the signal produced by the tags and the distance of transmitted signal.

#### *2.3.2. Portable PIT tag tracker*

A portable PIT tag tracker allows the user to detect the presence of a PIT tag from a distance of 40-60cm depending on the orientation between reader and tag (Cucherousset et al. 2008; Cucherousset et al. 2010). The tags identification number is displayed and recorded. The relatively short distance of tag detection distance means that the location of the tag (and the fish if implanted with a PIT tag) is known. The portable PIT tag tracker was used to observe the locations of tagged fish to the scale of the patch. The HDX portable PIT tag antenna was a HDX Backpack Reader from Oregon RFID Pte. Ltd. USA.

## *2.4 Fieldwork methodology*

This section describes field methodologies and the sources of data collection used during this investigation and are complimentary information when reading chapter-specific methodology.

### *2.4.1 Discharge and temperature*

Measurements of water temperature (°C) were provided from a salmon counting research station upstream of the site (Game and Wildlife Conservation Trust, East Stoke, UK). Temperature recordings were taken every 15 minutes and were averaged for mean water temperature for the hour for input into the model. Discharge ( $\text{m}^3.\text{s}^{-1}$ ) was measured from a station (NRFA Reference 440001) just upstream of the study site but within the Mill Stream and data was kindly provided on request from the Environment Agency.

### *2.4.2 Habitat characteristics – HABSCORE*

A semi-quantitative survey of each patch's environmental characteristics including substrate, flow characteristics, bankside and overhead vegetation cover and aquatic macrophyte cover was performed on a monthly basis. The habitat characteristics assessed follows the HABSCORE methodology commonly used to assess habitat quality in salmonid rivers (Milner et al. 1998).

### *2.4.3 Channel and river characteristics*

Detailed measurements of channel characteristics of elevation and location were recorded using a differential Global Positioning system (dGPS) Leica 500, Leica Geosystems, rover and base stations. Detailed recordings ( $\pm 1$  cm) of location of channel and patch boundaries, river bed elevation and water height elevation were taken at times of normal, high and low discharge within the Mill Stream and used to calibrate the hydrodynamic flow model.

#### 2.4.4 Electric fishing & population measurements

A two-pass depletion electric fishing methodology allowed for the measurements of fish biometrics and estimation of population numbers. Each stretch was fished one at a time and stretch 1 was always fished first before moving to the next upstream stretch to minimise disturbance. Prior to being fished, two stop nets (3cm x 3cm gaps) were placed at the downstream and upstream ends of the stretch to be fished to prevent movement of fish in and out of the stretch during the survey (see Figure 2.3 for stretch locations). The stretch was fished using 50Hz pulsed DC equipment, usually in a single anode and double catch net configuration. Stunned fish were netted and removed from the stretch and kept in aerated holding containers. The stretch was fished once before returning for a second pass. The relative numbers of fish caught in the 1<sup>st</sup> pass and 2<sup>nd</sup> pass allowed for the estimation of the total stretch population (e.g. depletion). The probability of capturing a fish, the estimate and variance of population numbers were calculated by the three following equations from Seber & Cren (1967):

$$P(\text{capture}) = \frac{P_1 - P_2}{P_1}$$

Where  $P(\text{capture})$  is the probability of capturing a fish during the electric fishing survey;  $P_1$  is the number of fish caught in the first pass;  $P_2$  is the number of fish caught in the second pass.

$$\hat{N} = \frac{P_1}{P(\text{capture})} = \frac{P_1^2}{(P_1 - P_2)}$$

Where  $N$  is the estimate for the total number of fish in that stretch.

$$var(\hat{N}) = \frac{P_1^2 P_2^2 (P_1 + P_2)}{(P_1 - P_2)^4}$$

Where  $var(N)$  is the variance in population estimate.

If the depletion is poor (the number of fish caught in the second pass is nearly as high as the number of fish caught in the first pass), the probability of capture is low and there is low confidence in the population estimate (Seber & Cren 1967). Poor depletion when electric fishing a stretch may be due to a multitude of factors including but not limited to difficult environmental conditions making catching fish difficult (e.g. high velocity or high depth), inexperienced electric fishers or low population numbers to begin with. The electric fishing team always consisted of experienced practitioners from the Game and Wildlife Conservation Trust and Bournemouth University so poor depletion due to inexperience practitioners is unlikely. Stretches with poor depletion,  $P(\text{capture}) < 0.2$ , were removed from analysis when validating IBM patterns.

All fish caught in the electric fishing surveys had their 1) species, 2) stretch they were caught from, 3) length (nearest mm) and 4) bodymass ( $\pm 0.1\text{g}$ ) recorded.

#### *2.4.5. Inserting PIT tags into fish for identification*

PIT tagging a fish is a regulated procedure and fieldwork was performed under Bournemouth University Home Office project license ‘Ecology of Freshwater fish’ PPL 30/2626. When PIT tagging a fish, fish were first anaesthetised in 2-phenoxyethanol (2PE) in 2008 and tricaine mesylate (MS222) in 2010 and 2011, before a scalpel was used to make a small incision close to the peritoneal cavity and a PIT tag inserted. Following the findings of Roussel et al. (2000), to ensure high survival of fish post tagging, salmonids with fork length below 90mm were implanted with the small PIT tag and larger fish (typically one year or older fish in this study) would be implanted with either the 12.5mm or the larger 23mm PIT tags.

Fish below 70mm were not implanted with a tag. Fish were then placed in a recovery, aerated tank and released back into the stretch they were caught from once they had fully recovered from the anaesthesia and the electric fishing survey was completed in that stretch.

#### *2.4.6. Tracking fish distribution*

The location of tagged fish (to the scale of a patch) was recorded using the portable PIT tag tracker. Following the method outlined in Cucherousset et al. (2010), a tracking survey involved the user entering the water and sweeping the antenna in the patch to detect the presence of any PIT tags. If the water depth was shallower than the maximum PIT tag detection distance, the antenna would not enter the water but if the water depth exceeded detection distance, the antenna loop would enter the water. Along with slow and careful user movement through the water, this minimised disturbance to the fish during the tracking. The direction of tracking events was a mixture of upstream and downstream.

To ensure that the locations of real and live fish were used to describe fish distribution at the scale of the patch, only the tags recorded in tagged fish that were recaptured at a later date were used; this removed the possibility of using tracking data from either dead fish or tags that had been ejected from the fish.

#### *2.4.7. Invertebrate densities*

Invertebrate drift nets (25 x 40 cm frame size, 500µm mesh size) were setup in a specific patch within each stretch (1-7) at monthly intervals throughout the field period with samples taken at three points throughout the day (dawn, noon and dusk) to measure the diel trend in invertebrate drift. Drift nets were placed at the same locations in the 2008 and 2010 field seasons, with the mouth of net tangential to the direction of channel flow. The bottom of the net frame was set flush with the riverbed. Depth, velocities at net mouth at a  $\frac{1}{4}$ ,  $\frac{1}{2}$  and  $\frac{3}{4}$  of channel depth were averaged out for a mean

velocity estimate and the exact duration of sampling was recorded (with the aim for a sampling duration of one hour). Estimates of benthic invertebrate densities were also collected at the same time using surber nets (30cm x 30cm); all riverbed substrate (up to an inch in depth) in the defined square were cleaned in the flow immediately upstream of the collecting net. To avoid affecting the collection of invertebrate drift, the location of the surber net setup was down stream of the drift net but still within the same patch. Each surber net survey was held in a different area of riverbed to avoid sampling an area that had already been cleaned. Invertebrates collected in the drift net were preserved in a 70% industrial methylated spirit (IMS) solution and were classified (family) and had their body length measured (nearest 0.1mm).

#### 2.4.8 1-D flow model

Riverbed gradient, water depth and discharge measurements were used to calibrate a 1-D flow model to estimate mean patch velocity and depth. This information was provided along with the 2008 dataset. A description of the flow model used is provided. Predictions were based on river discharge, and accounted for spatial and temporal variability in vegetation cover. The hydrological model is based on a step backwater solution of the 1-D gradually varied flow equations (French 1986), which can be written as:

$$\frac{dh}{dx} = \frac{S_0 - S_f}{1 - Fr^2}$$

where  $h$  = flow depth,  $x$  = distance along the downstream channel axis,  $Fr$  is the Froude number,  $S_0$  is the bed slope and  $S_f$  is the friction slope.

Friction slopes are estimated using the Manning resistance law:

$$S_f = \frac{V^2 n^2}{h^{4/3}} = \left(\frac{Q}{W}\right)^2 \left(\frac{n}{h^{5/3}}\right)^2$$

where  $V$  = flow velocity,  $Q$  = discharge,  $W$  = channel width and  $n$  = Manning friction coefficient (quadratic of % macrophyte cover).

Values of  $n$  were defined as a quadratic function of the percentage of the riverbed covered by vegetation within each patch. This relationship was calibrated using measurements of percentage vegetation, flow depth and velocity made throughout the study reach at a known discharge. This approach is termed quasi 1-D because a uniform value of  $S_f$  is assumed at each stretch. This uniform value is determined by integrating equation 2 over the distribution of depths and  $n$  values at each section (note that some sections contain two patches and in each patch a constant value of  $n$  is assumed).

## 2.5. Description of fieldwork and datasets

### *2.5.1 overview*

This thesis uses three primary fieldwork seasons (2008, 2010 & 2011) as data sources. Data on Mill Stream environment and fish behaviour in 2008 is owned by Bournemouth University. The author carried out the two subsequent fieldwork seasons in 2010 and 2011. In 2010, the effect the removal of aquatic macrophyte on salmonid populations was investigated whilst the 2011 field season observed the predator-prey interactions between pike and salmonids. The fieldwork methodology in these years closely followed the methodology used in 2008 to ensure an element of compatibility when using the data to parameterise and validate the developed IBM. In each field season, electric fishing surveys and PIT tag tracking collected the following characteristics of the salmonid population: 1) total population size, 2) population per stretch, 3) patch location of tagged fish, 4) fish bodymass and 5) fish length. The following environmental characteristics were also collected: 1) discharge, 2) water temperature, 3) invertebrate density, 4) semi-quantitative descriptions of habitat (HABSCORE) and 5) water depth in each patch. See the methodology section in each chapter for further details into fieldwork relevant to that specific chapter.

### *2.5.2. The virtual environment - 2008 and 2010 datasets*

There are two environmental datasets used throughout this investigation and these are derived from observed environmental conditions at the study site in the two field seasons carried out in 2008 and 2010. No environmental management occurred in the Mill Stream during the 2008 period (with the exception of reduced flow towards the end, but this is treated as an independent ‘environmental period’ during model analysis) and as such the period of natural flow in the 2008 environmental dataset is representative of the Mill Stream under natural conditions. In 2010, aquatic macrophyte in the Mill Stream was removed just prior to recording environmental



parameters (see chapter 6). The virtual environment in the salmonid IBM was parameterised using the 2008 or 2010 environmental datasets (see chapter methodology for information about which environmental dataset that chapter was using).

### *2.5.3. 2008 – natural conditions and a period of reduced flow*

The water temperature range was from 12.2 to 19.6°C (Figure 2.4). The discharge was under natural conditions until the last two weeks on the field period when the discharge was severely reduced by closing the fluvium (Figure 2.4). The stretches with the greatest mean water depths were stretches 4, 5 & 6 with stretches 1, 2, 3 & 7 being shallower (Figure 2.5). This same stretch pattern was seen in average estimated water velocities; the deeper stretches had slower water velocities than the shallower stretches and this was reflected in the mean area of patch that had flowing water (runs) as opposed to slack water (Figure 2.5). Stretches 1, 2, 3 & 4 had higher densities of drifting invertebrates than the remaining stretches with the invertebrates predominately aquatic in origin except for stretch 7 that had higher densities of terrestrial invertebrates in the size category 1-3mm (Figure 2.6). There was fairly high aquatic macrophyte cover in all the stretches with highest cover observed in stretch 2 (Figure 2.7). Pike were recorded in all the stretches but the highest densities were observed in stretch 5 where the density of large pike (Fork Length > 218mm) was 5 times higher than in any other section (Figure 2.7).

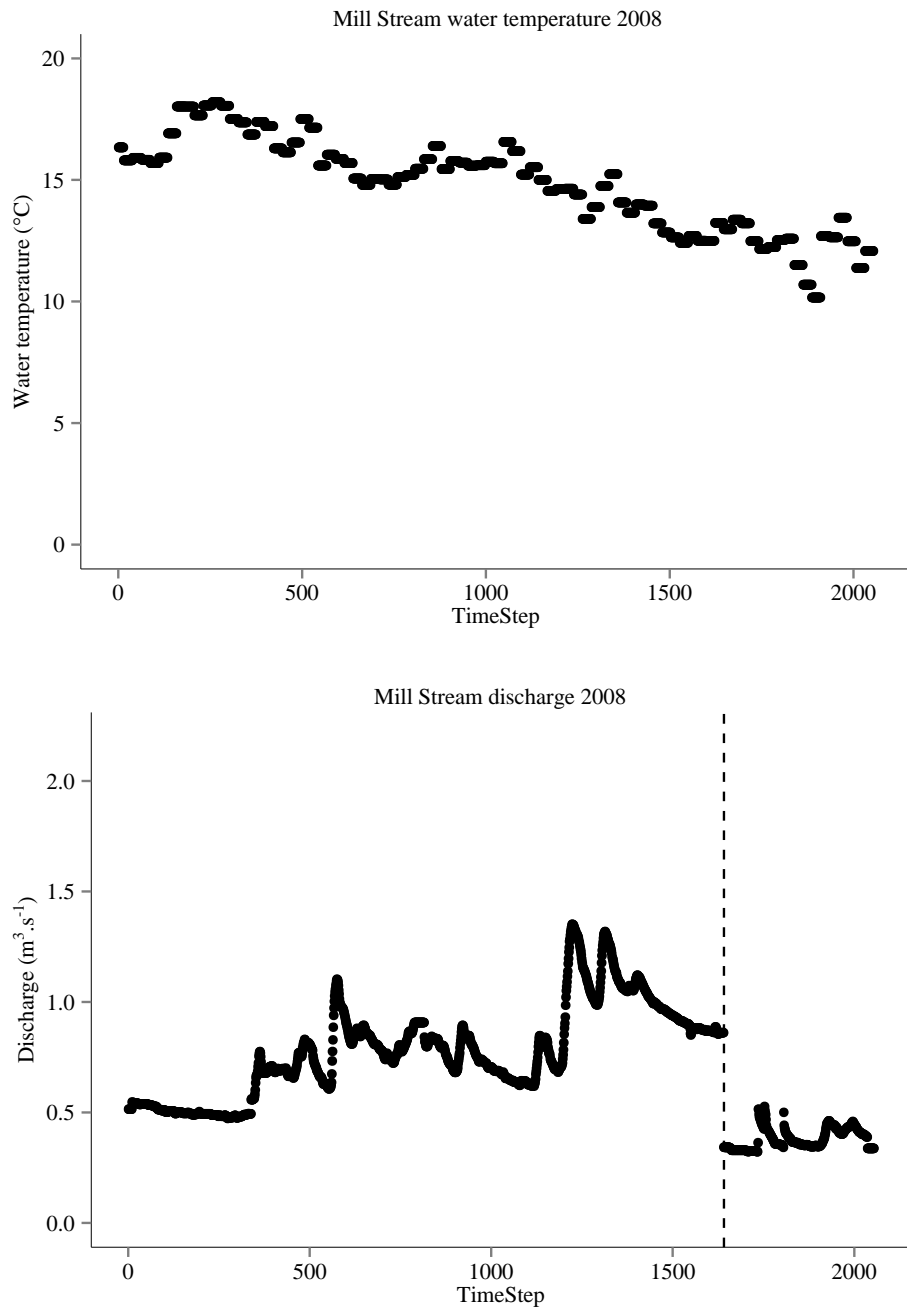


Figure 2.4 Mill Stream mean water temperature ( $^{\circ}\text{C}$  – top graph) and discharge (cumecs – bottom graph) for the July – October 2008 study period. Timesteps (hour) relate to the time in the model. Mean water temperature is an average of water temperature readings taken every 15 minutes at the salmon counting station (upstream) operated by the Game and Wildlife Conservation Trust (East Stoke, UK). Discharge recordings are provided by the Environment Agency (recording station NRFA 44001). The dotted line represents the moment the fluvarium was closed to reduce the flow entering the Mill Stream, moving from a natural flow regime to a regime of reduced flow.

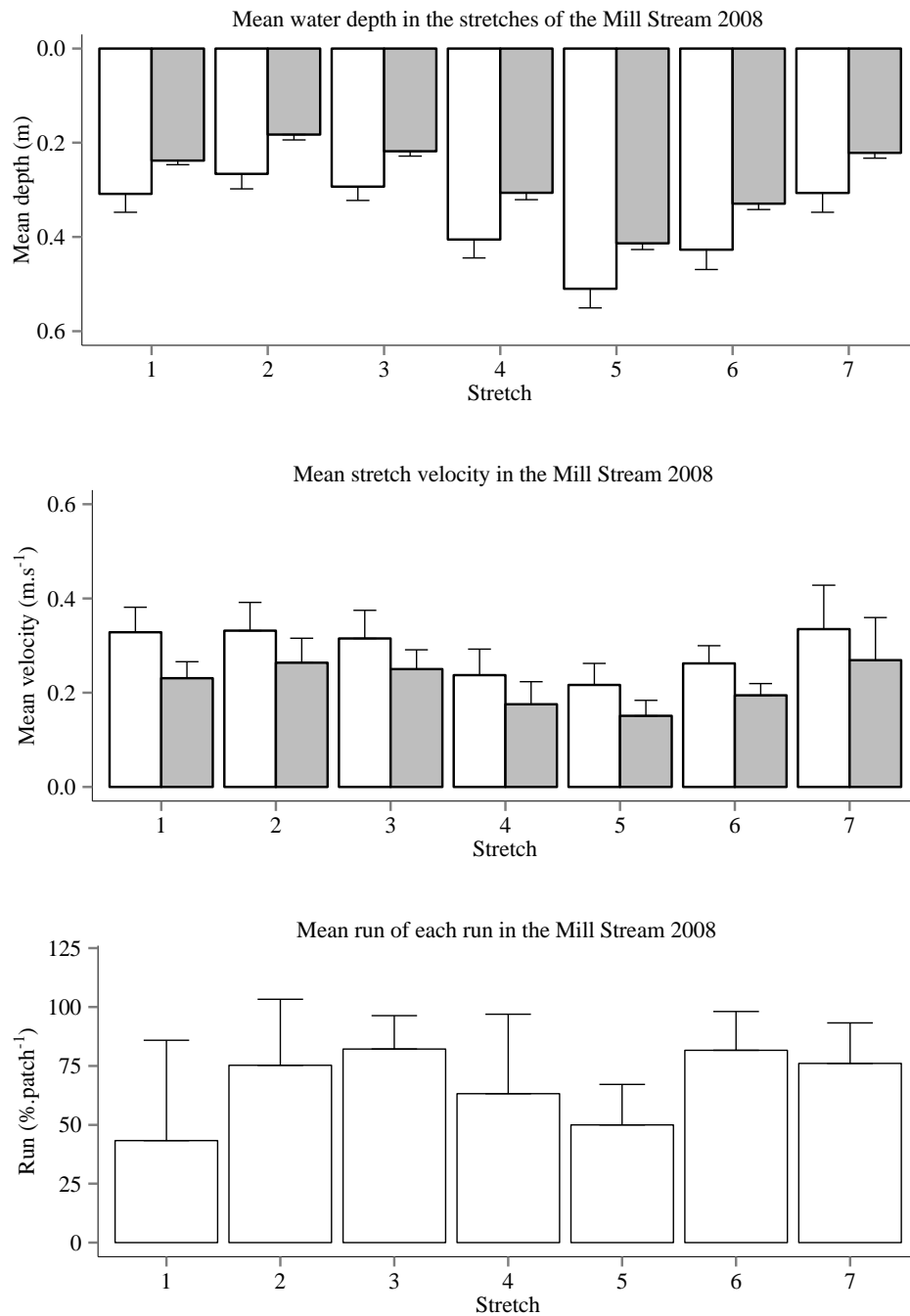


Figure 2.5 The mean channel conditions of stretches in the study site between July – October 2008 of water depth (m), water velocity ( $\text{m.s}^{-1}$ ) and percentage of running water (as opposed to slack) ( $\text{%.patch}^{-1}$ ). Errors bars show S.D. from the mean. The flow regime was unmodified for the first 3 months (white bars) but severely reduced in the final 3 weeks of the study period (grey bars). Depth and velocities were calculated from a 1-D hydrodynamic flow model and the area of running water per patch was recorded from a semi-quantitative HABSCORE survey performed throughout the fieldwork season ( $n=3$ ).

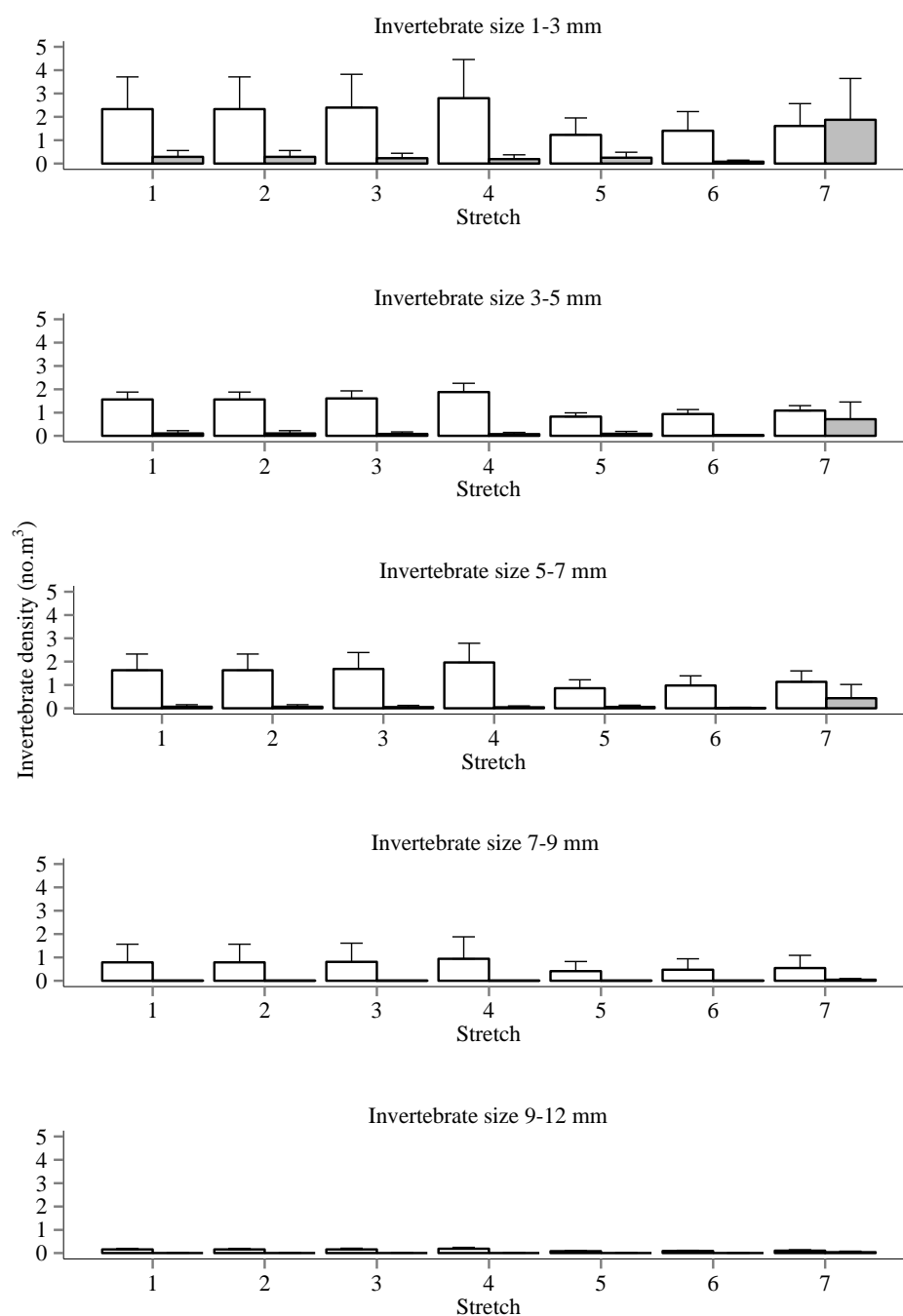


Figure 2.6 Inter-stretch differences of resource availability (drifting invertebrates) between July – October 2008. The size distribution and mean density (ind.m<sup>-3</sup>) of drifting invertebrates are used to quantify the amount of energy available to drift feeding fish. Errors bars show S.D. from the mean with white bars indicating invertebrates that are aquatic in origin with those terrestrial in origin shown in grey. Size distribution are estimated from drift nets samples (n=9 for each stretch) but densities were calculated using a correction coefficient (see chapter 3 – ‘resource density’) to overcome known sampling errors associated with drift net sampling when estimating densities (Faulkner & Copp 2001).

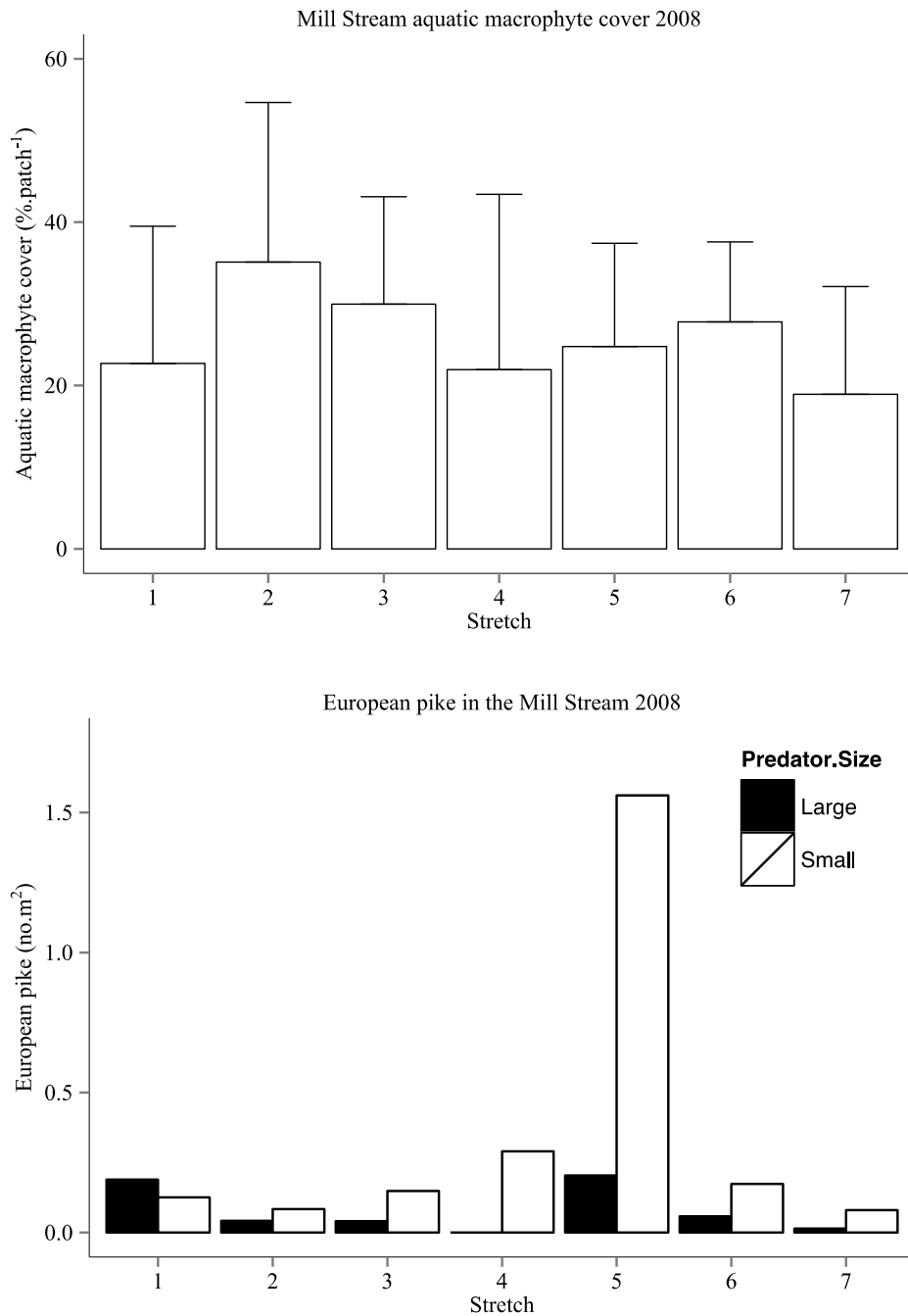


Figure 2.7 Inter-stretch habitat cover (aquatic macrophyte) and predator densities (European pike *Esox lucius*) in the Mill Stream over the period from July - October 2008. Aquatic macrophyte cover is recorded as % cover per patch from semi-quantitative HABSCORE surveys (n=3) and error bars indicate S.D. from the mean. Predator densities are the mean of number of pike caught during electric fishing surveys (n=4) and are divided into two size categories based on their fork length (FL); large (FL > 210mm) and small (FL < 210mm).

#### 2.5.4 The fish population in 2008

The population bodymass of caught young-of-year (YoY) Atlantic salmon, YoY brown trout and one-year-old (1+) brown trout at the start of the field observation period in 2008 (TimeStep = 1) was  $4.65\text{g} \pm 1.33$ ,  $7.89\text{g} \pm 2.19$  and  $68.16\text{g} \pm 14.97$  respectively (mean  $\pm$  S.D.) (Table 2.2, Figure 2.8, Figure 2.9 and Figure 2.10). The spatial distribution of the different fish across the different stretches showed an uneven distribution; the highest densities of YoY fish were found in stretches 2, 3 and 7 whereas the larger 1+ fish preferred stretches 1-4. Stretch 5 had the lowest densities of YoY fish and no 1+ brown trout were caught in stretch 6. The mean bodymass of fish across the stretches showed slight variation around the population mean. For each fish class, the mean population bodymass increased over the studied period at each subsequent population survey.

Table 2.2 The bodymass (g) (mean  $\pm$  S.E.) of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the Mill Stream estimated from electric fishing surveys in 2008 with the number of fish caught indicated in brackets.

Fish	Population survey			
	1	2	3	4
YoY Atlantic Salmon	$4.65 \pm 0.13$ (111)	$6.93 \pm 0.29$ (24)	$8.21 \pm 0.42$ (32)	$8.82 \pm 0.42$ (29)
YoY brown trout	$7.89 \pm 0.33$ (44)	$10.88 \pm 0.64$ (27)	$13.96 \pm 0.73$ (29)	$14.91 \pm 0.92$ (28)
1+ brown trout	$68.16 \pm 2.88$ (27)	$72.72 \pm 3.19$ (25)	$83.95 \pm 5.41$ (17)	$86.40 \pm 5.07$ (16)

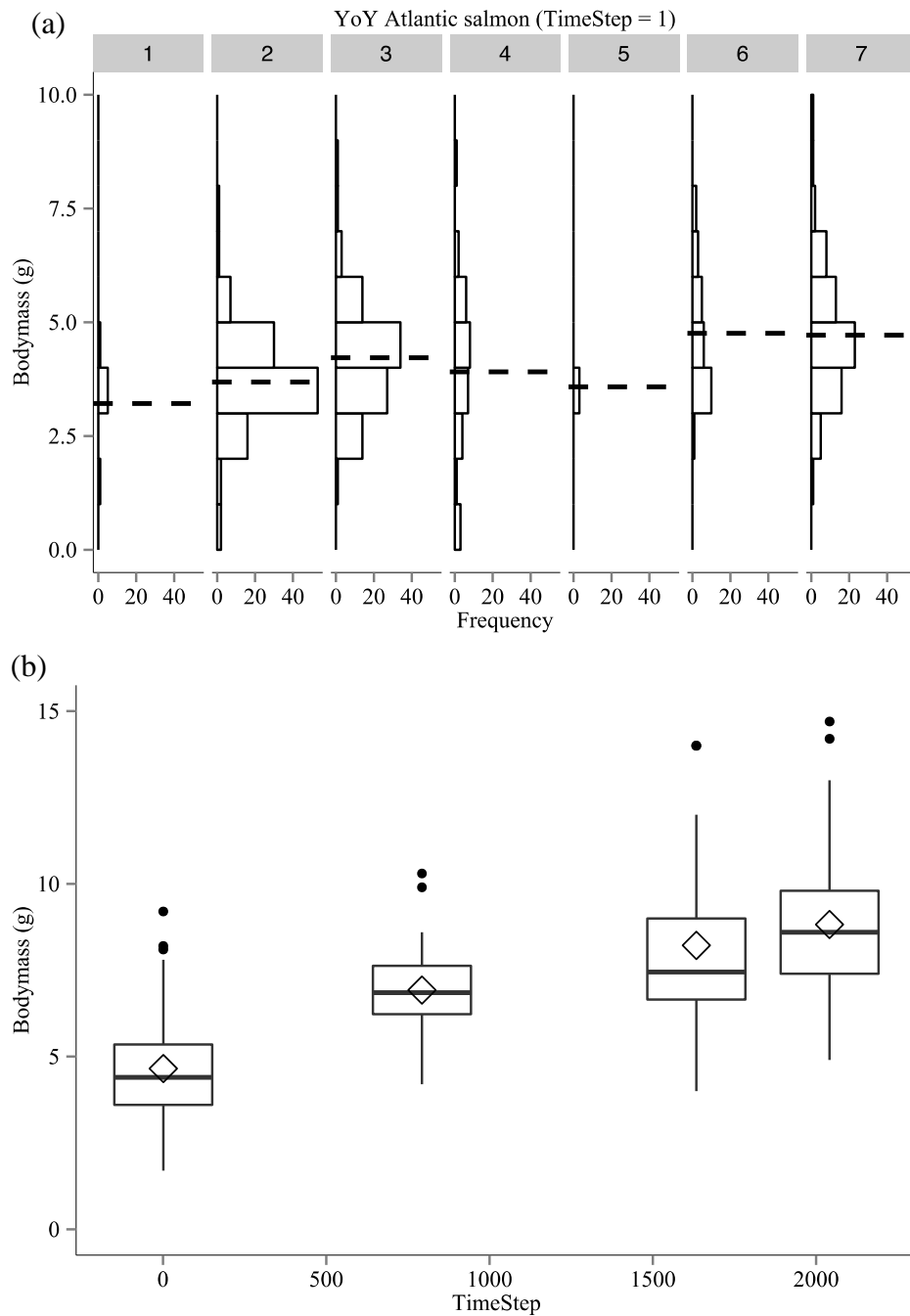


Figure 2.8 The body size (g) distribution of young-of-year (YoY) Atlantic salmon (*Salmo salar*) in the Mill Stream at the start of the study period (2008) across the different stretches (a – top graph) and the change in bodymass (growth) of the entire population through the study period (b – bottom graph). Numbers in the grey boxes indicate the stretch number in (a). Dashed lines and the diamond symbols show the distribution mean in (a) and (b) respectively.

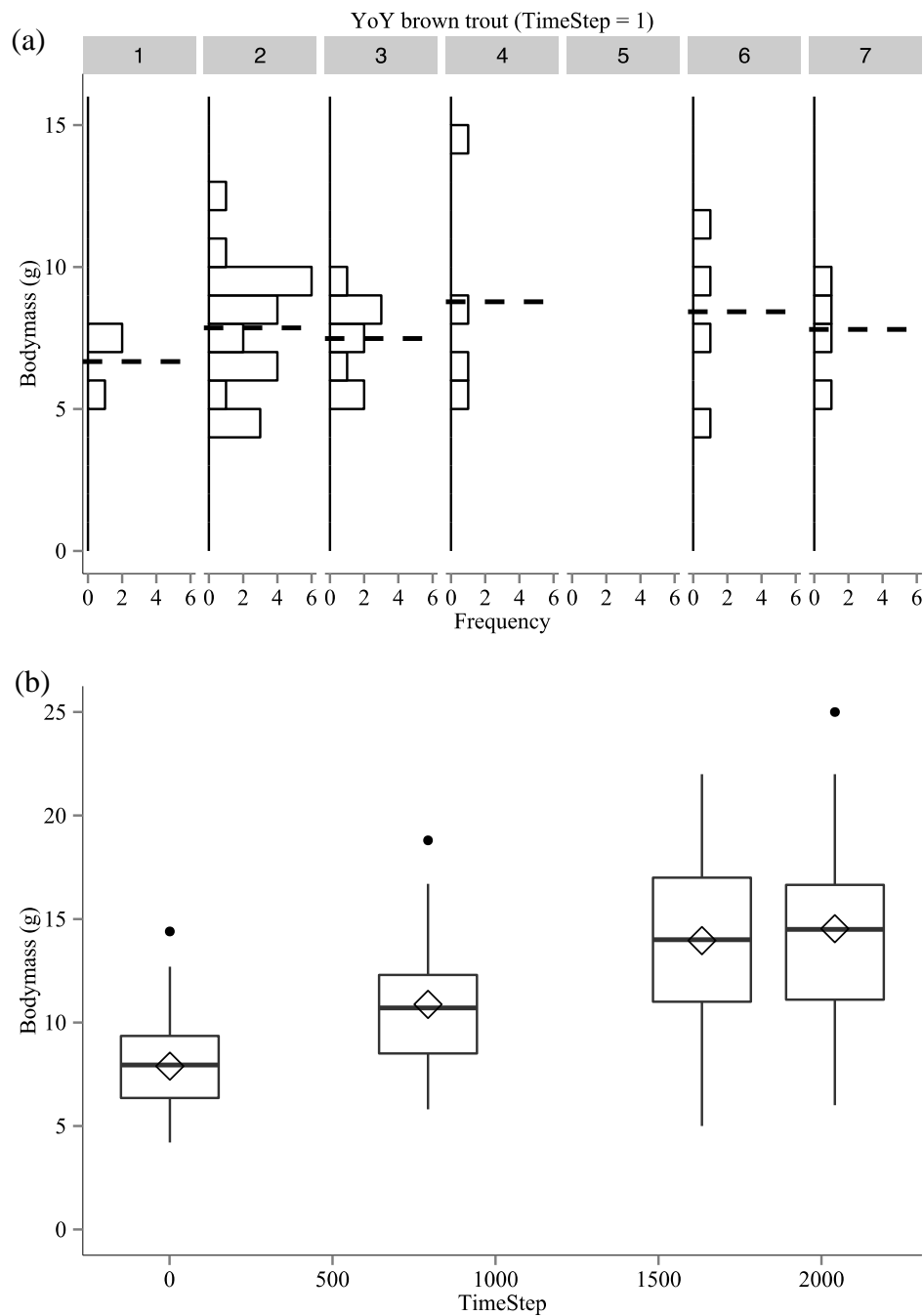


Figure 2.9 The body size (g) distribution of young-of-year (YoY) brown trout (*Salmo trutta*) in the Mill Stream at the start of the study period (2008) across the different stretches (a – top graph) and the change in bodymass (growth) of the entire population through the study period (b – bottom graph). Numbers in the grey boxes indicate the stretch number in (a). Dashed lines and the diamond symbols show the distribution mean in (a) and (b) respectively.



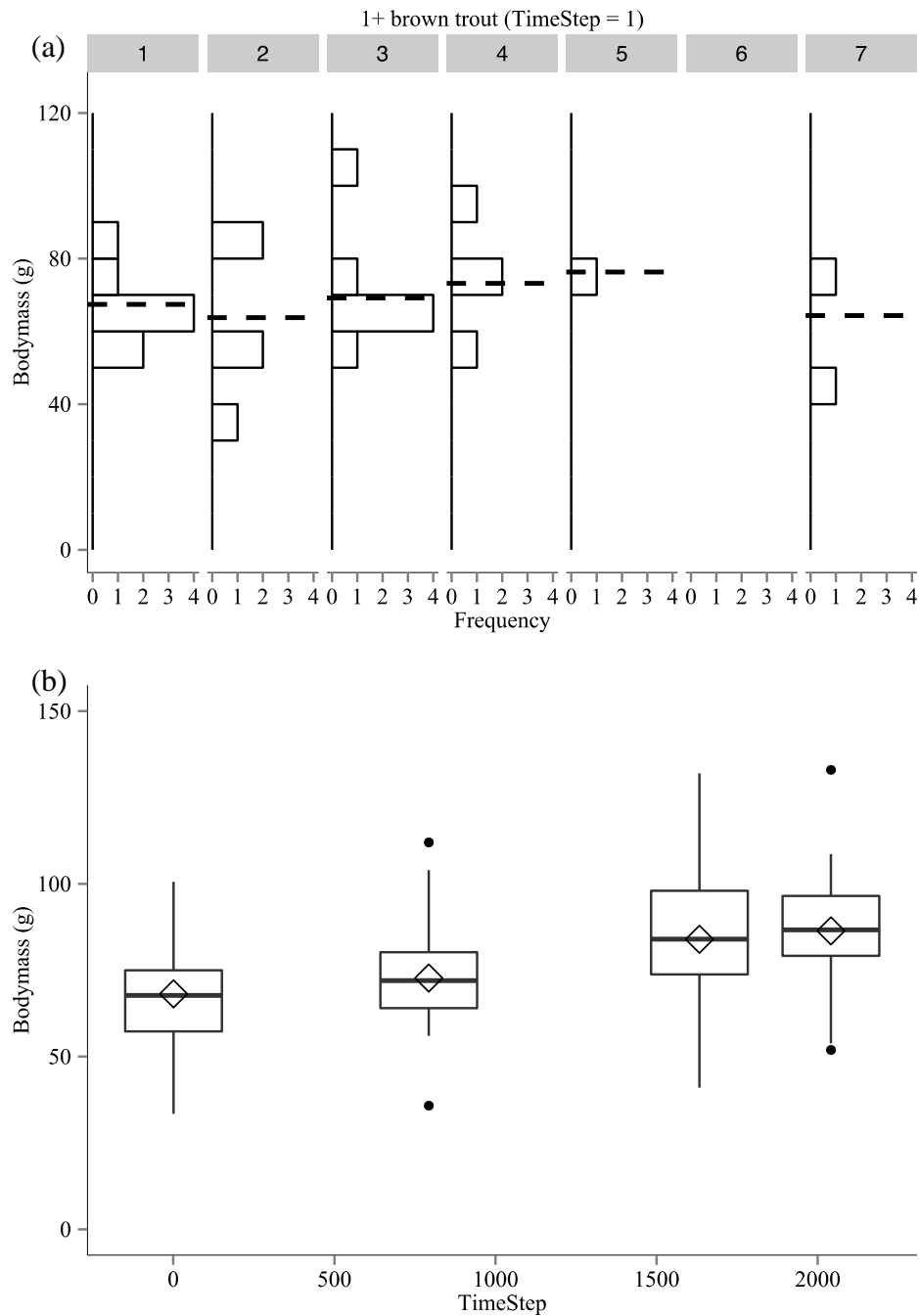


Figure 2.10 The body size (g) distribution of one-year-old (1+) brown trout (*Salmo trutta*) in the Mill Stream at the start of the study period (2008) across the different stretches (a – top graph) and the change in bodymass (growth) of the entire population through the study period (b – bottom graph). Numbers in the grey boxes indicate the stretch number in (a). Dashed lines and the diamond symbol show the distribution mean in (a) and (b) respectively.

#### 2.5.5 Management of aquatic macrophytes in 2010

Prior to the start of the recording of fish population parameters, the main aquatic macrophyte, *Ranunculus spp.*, was cut and removed from the system over a three-day period prior to environmental recording. *Ranunculus spp.* stands were cut ten centimetres (circa) above the substrate and were removed from the channel. *Ranunculus spp.* was the dominant aquatic macrophyte species but other aquatic macrophyte stands that were found within the main channel were removed as well.

The water temperature range was from 12.0 to 17.9°C (Figure 2.11). The discharge was under natural conditions and there are two distinct peaks caused by very intense local rainfall. The stretches with the greatest mean water depths are the same as in 2008 with stretches 4, 5 & 6 being deeper than stretches 1, 2, 3 & 7; the deeper stretches also had lower velocities than the shallower ones (Figure 2.12). The mean area of patches that had flowing water (runs) as opposed to slack water was higher in 2010 than in 2008 as all stretches (with stretch 5 the exception) had running water accounting for 80% of patch area. Stretches 1, 2, 3 & 7 had higher densities of drifting invertebrates than the other stretches; stretch 5 recorded very little invertebrate drift (Figure 2.13). The removal of aquatic macrophyte prior to environmental recording reduced the amount of aquatic macrophyte cover when compared to 2008 (Figure 2.7 & Figure 2.14). The aquatic cover in stretch 2 was still relatively high but this was composed of the stems remaining after the removal of aquatic macrophytes; the HABSCORE approach made no reference to the structural complexity of the aquatic macrophyte cover. No pike were caught in any of the four electric fishing surveys; the cause of this is unknown as there was no direct management of pike in 2010 or in the preceding years (Figure 2.14).

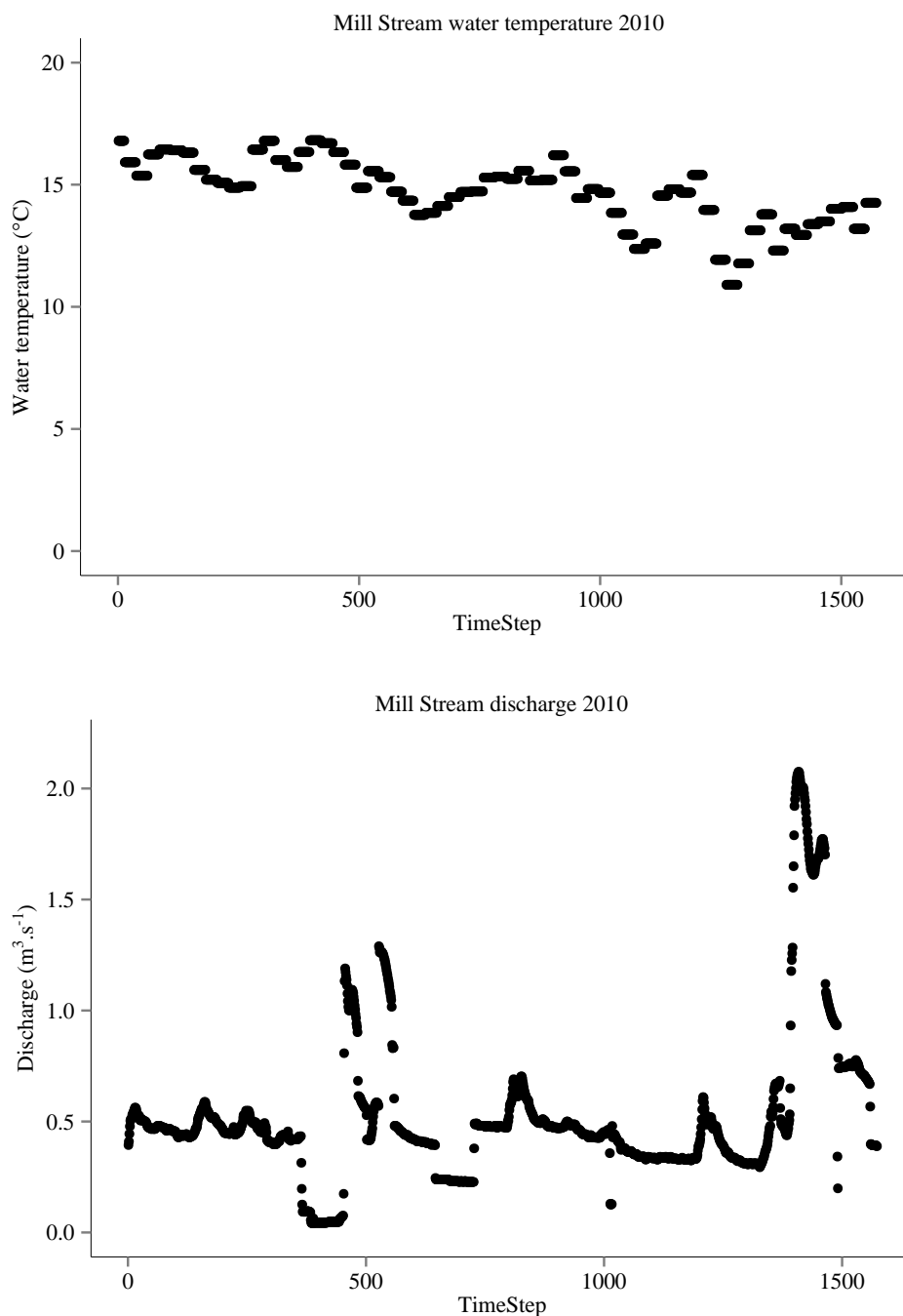


Figure 2.11 Mill Stream mean water temperature (°C – top graph) and discharge (cumecs – bottom graph) in the period between July – October 2010. Timesteps (hour) relate to the time in the model. Mean water temperature is an average of water temperature readings taken every 15 minutes at the salmon counting station (upstream) operated by the Game and Wildlife Conservation Trust (East Stoke, UK). Discharge recordings are provided by the Environment Agency (recording station NRFA 44001). The peaks in discharge represent events of high rainfall.

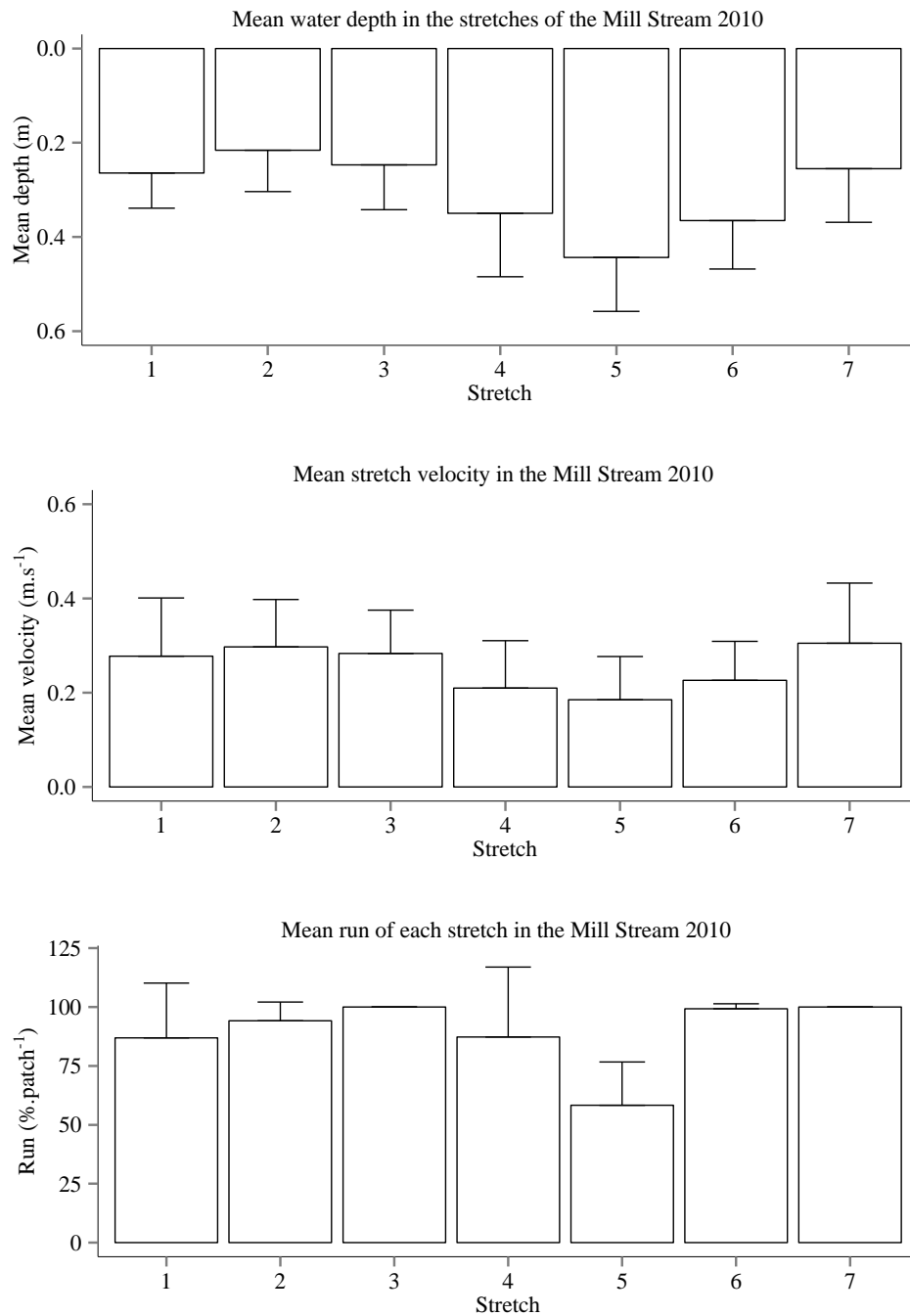


Figure 2.12 The mean channel conditions of stretches in the study site between July – October 2010 of water depth (m), water velocity (m.s<sup>-1</sup>) and percentage of running water (as opposed to slack) (%.patch<sup>-1</sup>). Errors bars show S.D. from the mean. Depth and velocities were calculated using a linear relationship between discharge:velocity and discharge:depth (at each patch) from estimates of depth and velocity in 2008 (calculated using a 1-D hydrodynamic flow model).

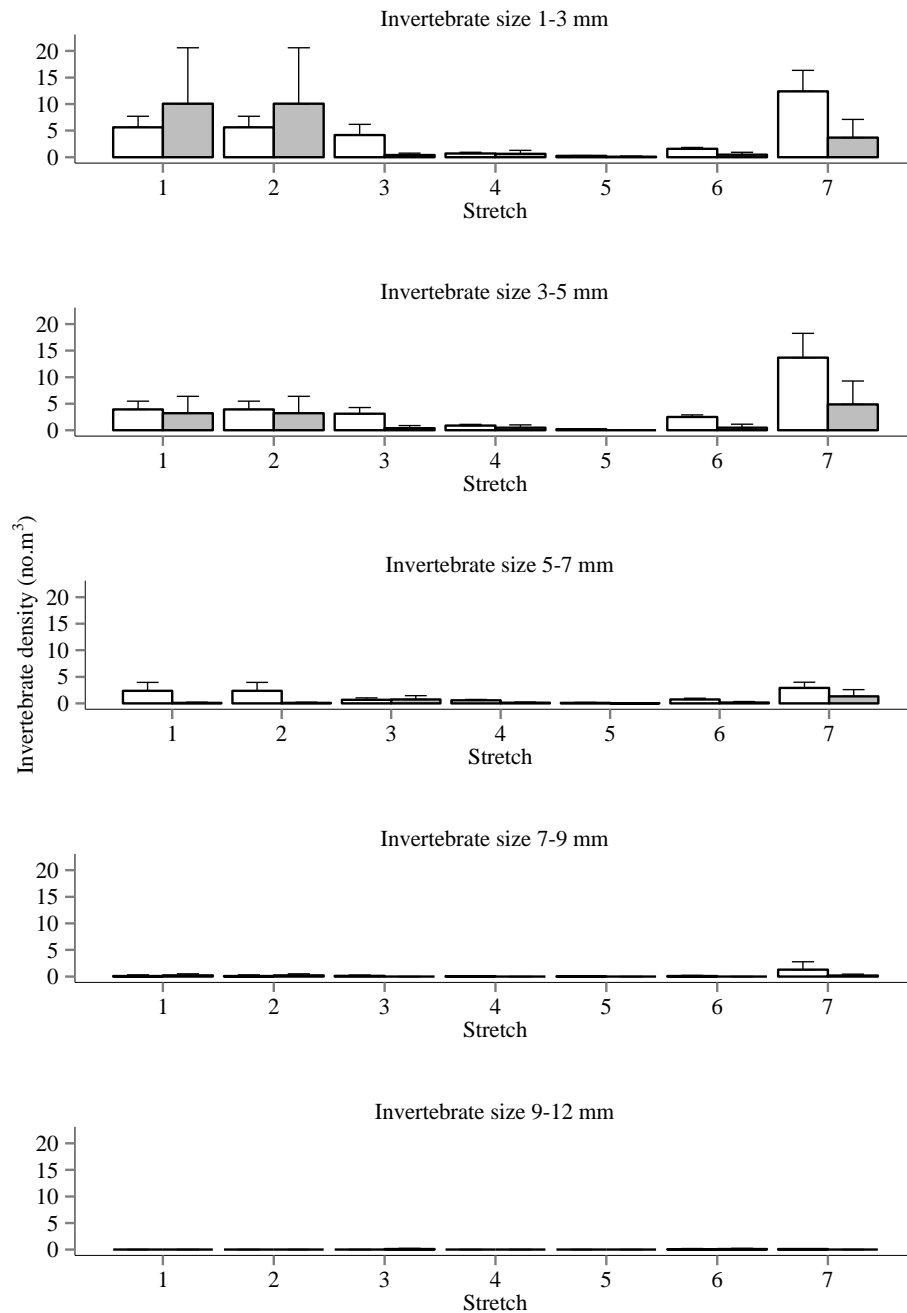


Figure 2.13 Inter-stretch differences of resource availability (drifting invertebrates) between July – October 2010. The size distribution and mean density (ind.m<sup>-3</sup>) of drifting invertebrates are used to quantify the amount of energy available to drift feeding fish. Errors bars show S.D. from the mean with white bars indicating invertebrates that are aquatic in origin with those terrestrial in origin shown in grey. Size distribution are estimated from drift nets samples (n=9 for each stretch) but densities were calculated using a correction coefficient (see chapter 3 – ‘resource density’) to overcome known sampling errors associated with drift net sampling when estimating densities (Faulkner & Copp 2001).

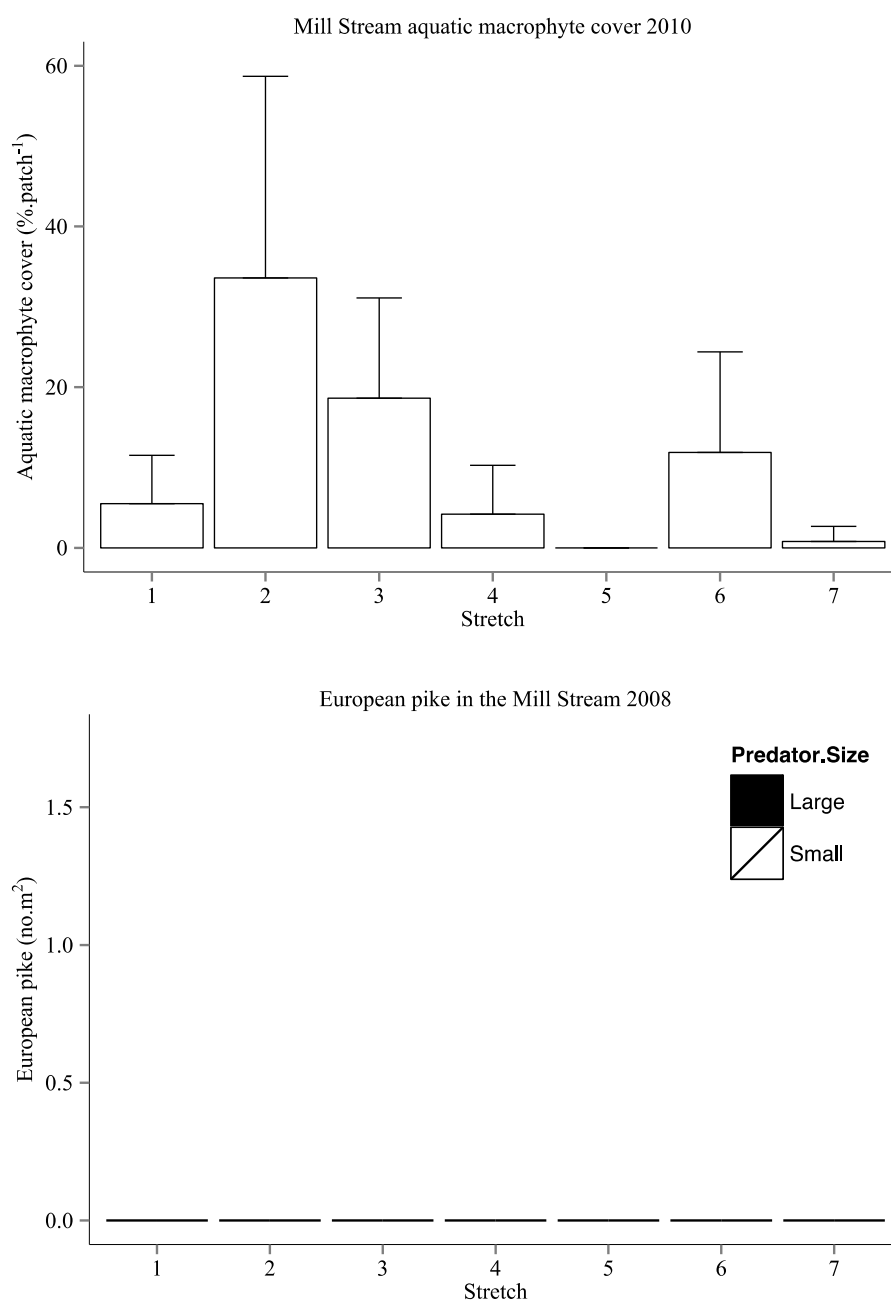


Figure 2.14 Inter-stretch habitat cover (aquatic macrophyte) and predator densities (European pike *Esox lucius*) in the Mill Stream over the period from July - October 2008. Aquatic macrophyte cover is recorded as % cover per patch from semi-quantitative HABSCORE surveys (n=3) and error bars indicate S.D. from the mean. Predator densities are the mean of number of pike caught during electric fishing surveys (n=4) and are divided into two size categories based on their fork length (FL); large (FL > 210mm) and small (FL < 210mm). All aquatic macrophyte cover was removed by manual cutting in the period leading up to the study season commencing. There was no management regime of pike numbers.

### 2.5.6 The fish population in 2010

The population bodymass of caught YoY Atlantic salmon, YoY brown trout and 1+ brown trout in the study site at the start of the field observation period in 2010 (TimeStep = 1) was  $5.53\text{g} \pm 1.45$ ,  $8.08\text{g} \pm 2.41$  and  $97.46\text{g} \pm 29.45$  respectively (mean  $\pm$  S.D.) (Table 2.3, Figure 2.15, Figure 2.16 and Figure 2.17 respectively). The spatial distribution of the different fish across the different stretches showed an uneven distribution; notably higher densities of YoY fish were found in stretch 2 whereas no 1+ fish were recorded being caught there. The highest densities of 1+ fish were in stretches 1 and 3. No YoY fish were caught in stretch 5 and 6. The mean bodymass of fish across the stretches showed slight variation about the population mean. For each fish class, the mean population bodymass increased over the studied period at each subsequent population survey.

Table 2.3 The bodymass (g) (mean  $\pm$  S.E.) of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the Mill Stream estimated from electric fishing surveys in 2010. The number of fish caught is shown in brackets.

Fish	Population survey		
	1	2	3
YoY Atlantic salmon	$5.53 \pm 0.16$ (83)	$7.88 \pm 0.25$ (89)	$9.13 \pm 0.26$ (114)
YoY brown trout	$8.08 \pm 0.33$ (52)	$10.72 \pm 0.44$ (66)	$13.83 \pm 0.64$ (72)
1+ brown trout	$97.46 \pm 4.66$ (40)	$107.44 \pm 5.92$ (38)	$116.58 \pm 6.58$ (39)

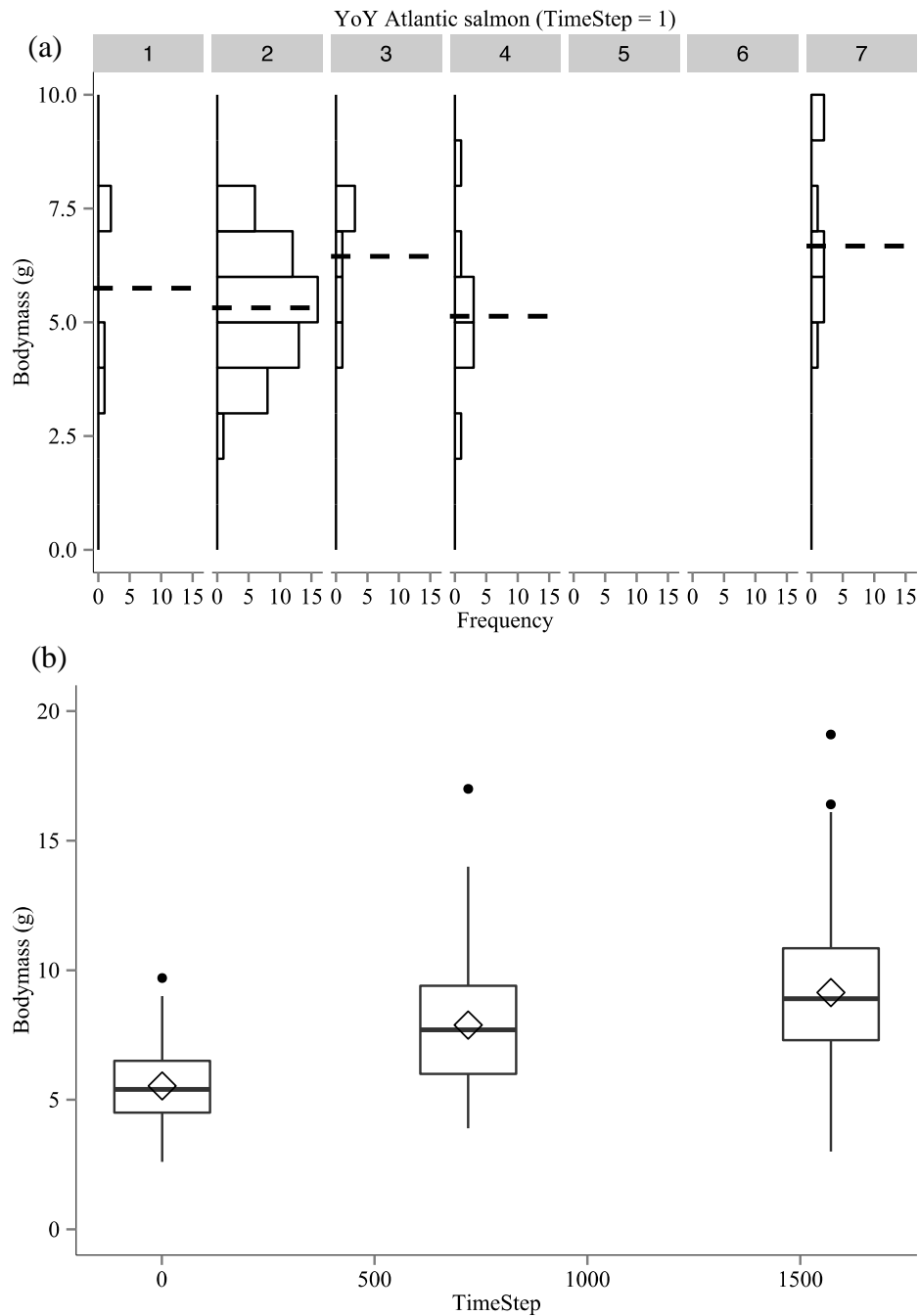


Figure 2.15 The body size (g) distribution of young-of-year (YoY) Atlantic salmon (*Salmo salar*) in the Mill Stream at the start of the study period (2010) across the different stretches (a – top graph) and the change in bodymass (growth) of the entire population through the study period (b – bottom graph). Numbers in the grey boxes indicate the stretch number in (a). Dashed lines and the diamond symbol show the distribution mean in (a) and (b) respectively.



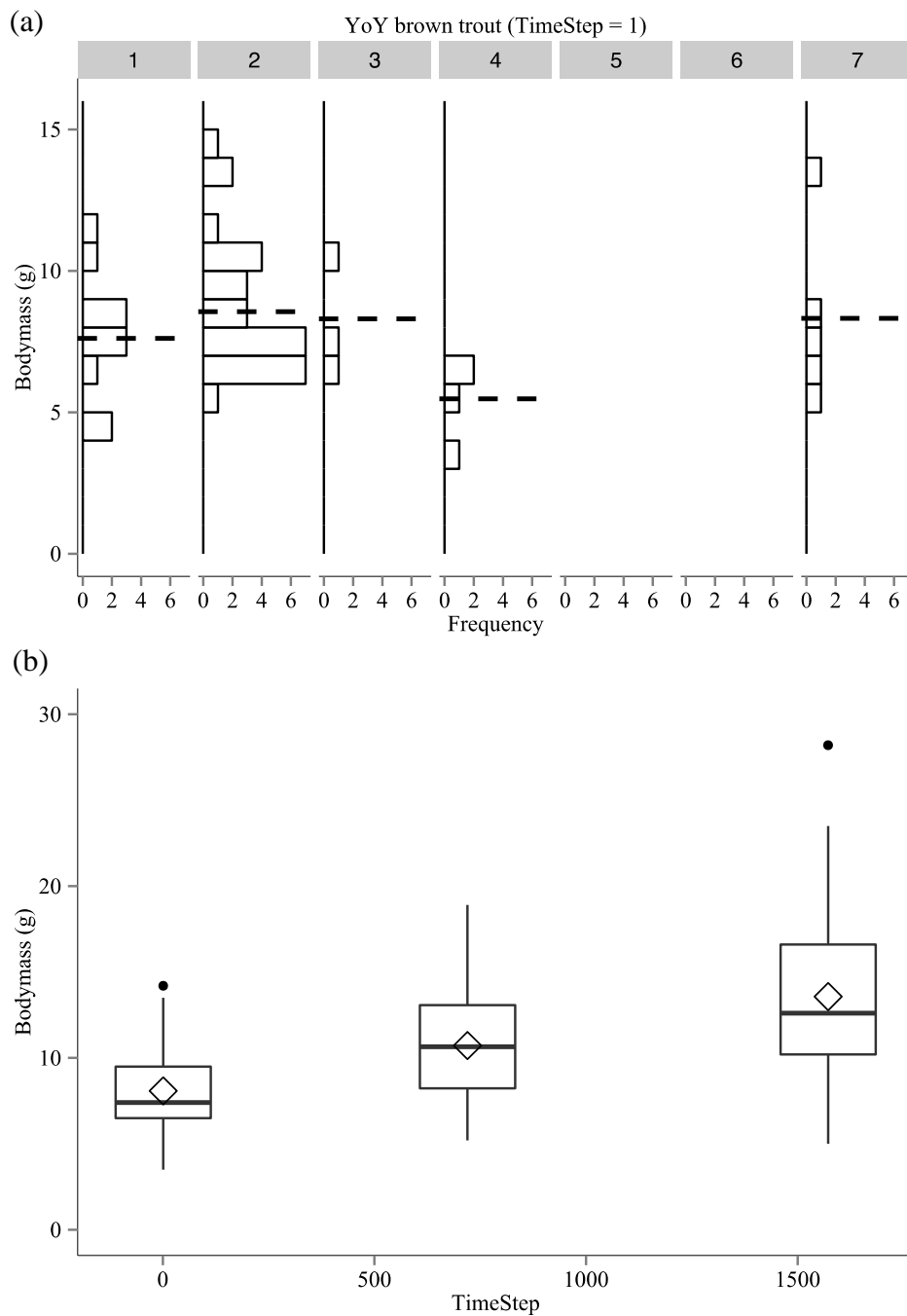
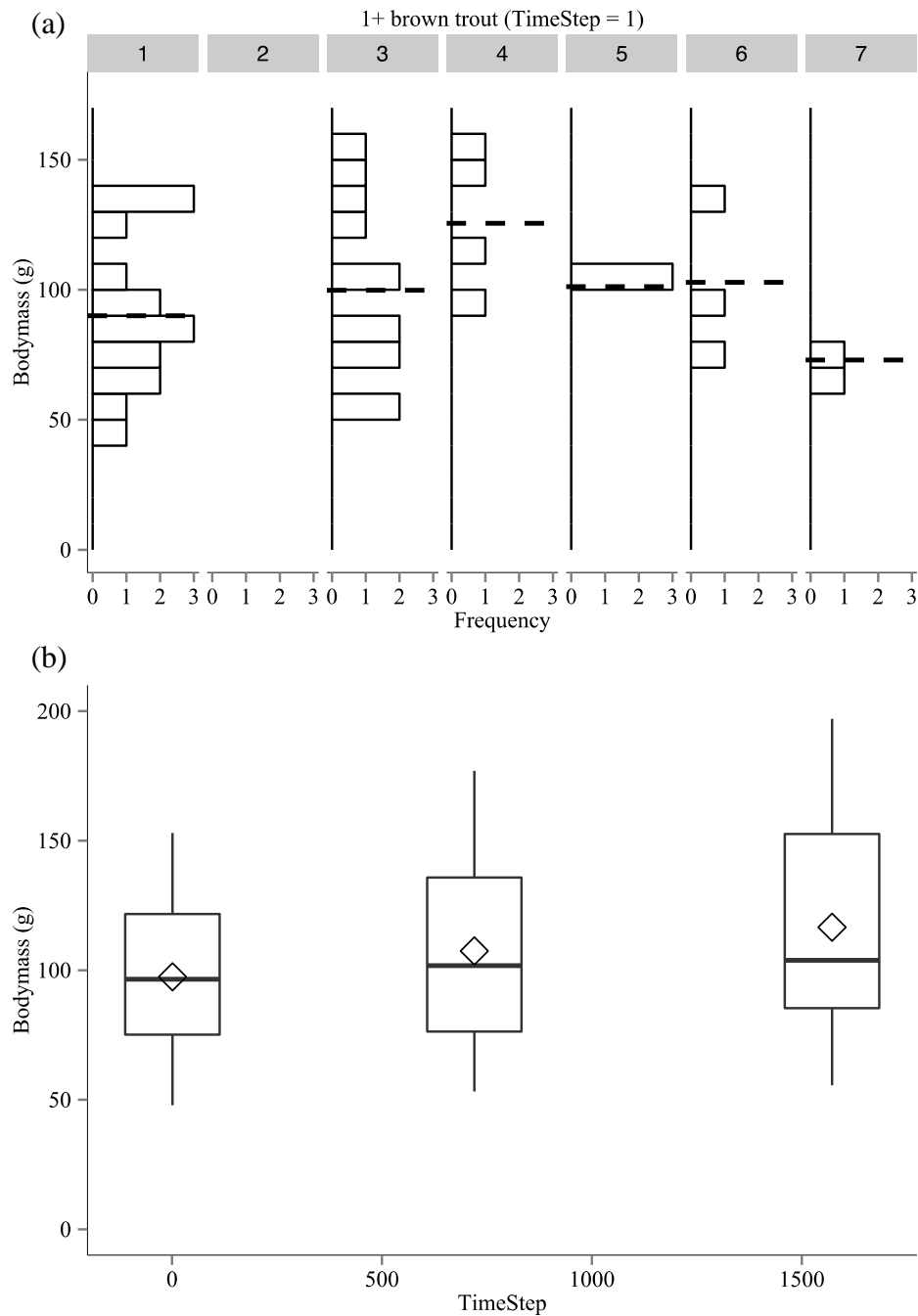


Figure 2.16 The body size (g) distribution of young-of-year (YoY) brown trout (*Salmo trutta*) in the Mill Stream at the start of the study period (2010) across the different stretches (a – top graph) and the change in bodymass (growth) of the entire population through the study period (b – bottom graph). Numbers in the grey boxes indicate the stretch number in (a). Dashed lines and the diamond symbol show the distribution mean in (a) and (b) respectively.



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### **3. Behaving like wild fish? A salmonid-specific individual-based model to predict fish growth and distributions**

#### **3.1 Introduction**

The health of global freshwater resources is under threat (Dudgeon et al. 2006). As open and dynamic systems, the types of threat are numerous and diverse, ranging from pollution to species introduction, habitat destruction and over exploitation (Dudgeon et al. 2006; Gozlan et al. 2005; Pinder et al. 2005; Xenopolous et al. 2005). One resource reliant on healthy freshwater ecosystems is fishing and its socio-economic significance is demonstrable; an estimated 14 million tonnes are harvested annually, the industry employs up to 20.7 million people globally and 60 millions of the total global population are reliant on it for their livelihood (Gozlan & Britton 2013). In the United Kingdom, the recreational fishing industry is worth an estimated UK£3 billion annually and is participated by nearly 4 million (Environment Agency 2004). Freshwater management must manage the threats by shifting away from traditional, reactive management to ecosystem-based fisheries and aquatic stewardship, and scientists need to provide them with robust and dynamic tools to achieve this (Francis et al. 2007).

Individual-based modelling (IBM) is a technique that simulates ecological realism, where ‘individuals’ operate within a virtual environment and display adaptive behaviours in response to individual, population and environmental parameters (Judson 1994; Grimm & Railsback 2005). These models distil the most relevant environmental and population parameters with a focus on the individual and their adaptive behaviours; modelling cumulative interactions at the individual level drive patterns at the population level. The incorporation of the adaptive behaviour of individuals in the model allows the population to respond realistically to environmental change and this makes it a powerful predictive tool (Judson 1994). IBMs

should be described following the Overview, Design and Details (ODD) of IBM description for clear communication (Grimm et al. 2006, 2010).

IBMs have proved to be successful in producing robust predictions for population dynamics under an environmental change. They have been a potent tool for coastal bird management (Toral et al. 2012; Stillman & Goss-Custard 2010) and are becoming increasingly popular with the management of other species (e.g. Railsback et al. 2009; Phillips et al. 2003). Railsback et al. (2003) used a trout individual-based model to show how the approach can be used to predict population responses more accurately than habitat-association models. A notable salmonid IBM is inSTREAM (Railsback et al. 2009), which is designed to produce multi-year (multi-generational) predictions over a large (catchment) scale. Its application at a smaller scale, both temporal (within year) and spatial (within reach) is limited and as such, not a useful model for small-scale privately owned fisheries. Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) fisheries in chalk streams in southern England are an example of small scale, privately owned fisheries that must manage the health of resident salmonid populations in light chalk stream environmental degradation and population decline (Whitehead et al. 2006, Environment Agency 2004).

Given the success of IBMS in coastal bird management (e.g. Stillman et al. 2001; Durrell et al. 2006), this chapter describes the first step in the development of a freshwater salmonid IBM specific to the chalk stream environment to advise management by predicting population responses to alternative management regimes. Chalk streams are highly productive habitats for salmonids (Berrie 1992; Wright & Symes 1999) and supports economically important ecosystem services including salmonid game fishing (Environment Agency 2004). This salmonid IBM will be spatially explicit and use bioenergetics to drive behavioural decisions of movement and time budgets. Results will be interpreted at the management-relevant

patterns of growth and distribution. Validation of model predictions will use both the ‘pattern-orientated modelling’ methodology (Grimm & Railsback 2005) and statistical tests.

## 3.2 Methodology

### 3.2.1 *Virtual environment*

The virtual environment in this model is parameterised to reflect environmental conditions in the Mill Stream in 2008. See chapter 2 for a detailed description of environmental parameters collected during the field study period.

### 3.2.2 *Model description*

#### 3.2.2.1 *Overview*

This salmonid IBM designed to predict behaviour of salmonids in a chalk stream environment. Brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) foragers interact within the virtual environment and perform adaptive behaviours in deciding their distribution and feeding behaviour. Behavioural decisions are defined by the bioenergetic consequences on forager growth and fitness. This IBM will be utilising the MORPH optimal-foraging, individual-based modelling platform (see Stillman 2008).

A field study of a natural salmonid population patterns in a chalk stream environment provides population and environmental data to parameterise and validate the model. The virtual habitat is modelled to resemble the observed environmental conditions and foragers are initialised from data collected on salmonid individuals at the start fieldwork.

#### *Purpose*

This salmonid IBM will be used to predict population distributions and the bioenergetics of the salmonid population measured as location and growth rates respectively. The model is designed to help fisher management understand regime effects during the dominant salmonid growth period.

The model will be validated by comparing patterns of virtual fish in the model with observed patterns of fish behaviour and growth collected from fieldwork data. IBM predictions can be validated by identifying several complimentary patterns as defined under the ‘pattern-orientated modelling’ methodology (Grimm & Railsback 2005). As a further step, in this investigation, there will be an effort to provide a quantitative, statistical validation of model predictions, to evaluate the ability of the model to predict fishery management-relevant patterns.

#### *Entities, state variables and scales*

MORPH describes entities in a hierarchal system with i) global, ii) patch and iii) forager entities described in a decreasing order of influence. Global variables apply throughout the system whilst patch variables are patch-specific. Forager variables define similarities and differences between the foragers.

#### *Spatial extent of the model*

The global environment replicates a 520 m long and a mean width of 4.8 m section of chalk stream. The environment is further classified at the ‘stretch’ and ‘patch’ level. Small mesohabitat ‘patches’ are defined as areas ( $39.7\text{m}^2 \pm 14.2$ , mean  $\pm$  S.E.) of similar environmental characteristics of water velocity, substrate, in-stream vegetation & terrestrial cover. A series of similar patches is then classified as a stretch and there are 7 stretches in the model (see chapter 2 for detailed description of the site the virtual environment is modelled on). The modelled system is represented as a closed system and virtual foragers cannot leave once they have entered.

#### *Global variables*

Global variables include the total duration of the model simulations and timesteps within the model are representative of an hour in length. Daylight and night are also modelled along with water temperature and discharge. Channel discharge was left natural for the first two months at which



discharge was severely reduced to mimic the environmental change of drought (Table 3.1).

#### *Patch variables*

Each patch has physical variables describing patch-specific parameters of i) area, ii) location, iii) the proportion of total area that is running or slack water, iv) mean depth and v) mean velocity for each time step. Sequentially located patches are grouped into stretches of similar macrohabitat with stretch variables of i) invertebrate prey densities and ii) predator (European pike, *Esox lucius*) densities (Table 3.2).

#### *Forager variables*

Each forager has variables pertaining to the forager's i) species, ii) age, iii) starting location, iii) tagged status, iv) initial bodymass and v) territory size (Table 3.3). Foragers are defined in two levels of classification. Foragers belong to *forager class* that describes their species and age and there are three forager classes (Table 3.3). Each forager class is further classified into *forager type* and this defines the stretch the forager must start in at the start of each model simulation (time step = 1). Forager types are used to define a virtual population that closely reflects the real population of salmonids observed during fieldwork. Analysis of both empirical data collected during fieldwork and virtual foragers within the IBM is done at the classification of forager class.

Table 3.1 The global parameters and formulas used to define the virtual environment in this salmonid individual-based model

Name	Formula	Source
Simulated Time Period	17 <sup>th</sup> Jul – 10 <sup>th</sup> Oct 2008	This study
Natural flow regime	17 <sup>th</sup> Jul – 23 <sup>rd</sup> Sep	This study
Reduced flow regime	23 <sup>rd</sup> Sep – 10 <sup>th</sup> Oct	This study
Time Step Length	1 (2040 total)	This study
Daylight length	13.72 ± 1.47	This study
Daylight	0 = night 1 = day	This study
Water Temperature °C	15.47 ± 1.49 (natural) 12.29 ± 0.86 (reduced flow)	This study
Discharge (Q m <sup>-3</sup> )	0.778 ± 0.207 (natural) 0.381 ± 0.046 (reduced flow)	This study

Table 3.2 The patch parameters and formulas used to define the virtual environment in this salmonid individual-based model (mean ± SD)

Name	Value	Source
Stretches (S)	1-7 (7 total)	This study
Patch number (P)	1-75 (75 total)	This study
Mean patch area (m <sup>2</sup> )	39.64 ± 14.15	This study
Mean run % per patch (%)	69.95 ± 27.44	This study
Mean water velocity (m s <sup>-1</sup> )	0.26 ± 0.08	This study
Mean water depth (m)	0.30 ± 0.10	This study
Mean aquatic drift densities per stretch (ind. m <sup>-3</sup> )	6.48(S1), 6.48(S2), 6.66(S3), 7.77(S4), 3.41(S5), 3.89(S6), 4.48(S7)	This study
Mean terrestrial drift densities per stretch (ind. m <sup>-3</sup> )	0.63(S1), 0.62(S2), 0.53(S3), 0.50(S4), 0.49(S5), 0.22(S6), 3.20(S7)	This study
Prey biomass per prey type i	W <sub>prey,1</sub> = 0.1082, W <sub>prey,2</sub> = 0.3435, W <sub>prey,3</sub> = 1.2154, W <sub>prey,4</sub> = 2.4677, W <sub>prey,5</sub> = 5.8425, W <sub>prey,6</sub> = 2.2741, W <sub>prey,7</sub> = 1.3733, W <sub>prey,8</sub> = 4.0064, W <sub>prey,9</sub> = 6.9803, W <sub>prey,10</sub> = 7.1369	This study
Prey Energy Density (KJ d.w. g <sup>-1</sup> )	22.13	This study
Mean Prey length (mm)	4.342 ± 2.1	This study
Large pike densities (FL>218mm, ind.m <sup>2</sup> )	0.189(S1), 0.042(S2), 0.041(S3), 0.000(S4), 0.204(S5), 0.058(S6), 0.145(S7)	This study
Small pike densities (FL<218mm, ind. m <sup>2</sup> )	0.126(S1), 0.840(S2), 0.148(S3), 0.290(S4), 1.561 (S5), 0.174(S6), 0.080(S7)	This study

Table 3.3 The forager parameters and values used to define young-of-year (YoY) and one-year-old (1+) Atlantic salmon and brown trout foragers

Forager Parameters	Value	Source
Total number of individuals	410	This study
YoY salmon,tagged (ind. per stretch)	5(S1), 22(S2), 10(S3), 13(S4), 1(S5), 18(S6), 18(S7)	This study
YoY salmon,untagged (ind. per stretch)	3(S1), 84(S2), 85(S3), 16(S4), 0(S5), 8(S6), 52(S7)	This study
YoY trout,tagged (ind. per stretch)	3(S1), 21(S2), 8(S3), 4(S4), 0(S5), 4(S6), 6(S7)	This study
YoY trout,untagged (ind. per stretch)	0(S1), 0(S2), 0(S3), 0(S4), 0(S5), 0(S6), 0(S7)	This study
1+ trout,tagged (ind. per stretch)	8(S1), 5(S2), 7(S3), 4(S4), 0(S5), 0(S6), 1(S7)	This study
1+ trout,untagged (ind. per stretch)	0(S1), 0(S2), 0(S3), 0(S4), 0(S5), 0(S6), 0(S7)	This study
Mean forklength of YoY fish (mm)	96	This study
Mean forklength of 1+ fish (mm)	186	This study
Length (Lsalmonid,mm) : Weight (Wsalmonid,g)	$FL_{salmonid} = 44.688 \cdot W_{salmonid}^{0.2861}$	This study
Territory Size (TS) (m <sup>2</sup> )	$\log_{10} \text{territory size (m}^2\text{)}$ $= 2.61 \log_{10} \text{length(cm)} - 2.83$	Grant & Kramer (1990),
TS of 1+ fish	3.04	This study
TS of YoY fish	0.54	This study
Standard and maximum Metabolic Rate (calories day <sup>-1</sup> )	$R_{standard}, R_{max} = a \cdot W^{b_1} \cdot e^{b_2 T}$	Elliott 1975a, 1975b
Digestion metabolic rate (calories day <sup>-1</sup> )	$R_{digestion} = R_{max} - R_{standard}$	Elliott 1975a, 1975b
Feeding metabolic rate (calories day <sup>-1</sup> )	$MR_{feeding} = R_{standard} + R_{digestion} + SC_{feeding}$	Elliott 1975a, 1975b
Resting Metabolic Rate (calories day <sup>-1</sup> )	$MR_{resting} = R_{standard} + R_{digestion} + SC_{resting}$	Elliott 1975a, 1975b
Energy loss through faeces and urea	31% of Cmax	Elliott 1975a, 1975b
Max Consumption Rate (calories day <sup>-1</sup> )	$C_{max} = a \cdot W^{b_1} \cdot e^{b_2 T}$	Elliott 1975a, 1975b
Swimming costs (calories day <sup>-1</sup> )	$SC = a \cdot W^{b_1} \cdot e^{b_2 T} \cdot e^{b_3 T}$	Elliott (1976), Hayes et al. (2000), Rand et al. (1993)
Handling Time (h)	$\frac{1}{2} * RD * \left( \frac{1}{V_{max}} + \frac{1}{Patch_{velocity}} \right)$	Hayes et al. 2000, Hughes et al. 2003
Maximum Speed (V <sub>max</sub> )	$V_{max} = 36.23 \cdot FL^{0.19}$	Hayes et al. (2000) from Jones et al (1974)
Capture Probability (CP)	$CP = 104.8 \cdot (151.9 \cdot Patch_{velocity})$	Piccolo et al. 2008
Capture Area (CA)	If $RD < Patch_{depth}$ $CA = 2 \cdot RD \cdot RD$ If $RD > Patch_{depth}$ $CA = 2 \cdot RD \cdot Patch_{depth}$	Railsback & Harvery (2002)

Reaction Distance (RD)	$RD = 12 \cdot PL_i(1 - e^{(0.2FL(cm))})$ At night, RD = 0	Hughes & Dill (1990) from Jones et. al 1(974)
Rate of encounter for each prey size (i) (RE)	$3600 \cdot$ $Density_{Prey,i} \cdot Patch_{velocity} \cdot CA$	This study
Capture rate for each prey size (i)	$CP \cdot \frac{RE}{1 + \sum_{i=1}^{Prey i} CP \cdot RE \cdot h}$	Hughes et al. (2003)
Prey Energy Density (kJ g dw <sup>-1</sup> )	22.13	This study
Condition Factor	1.19	This study
Specific Energy Density	$3.148 \cdot e^{0.332 \cdot CF} \cdot W_{salmonid}^{0.072}$	
Minimum prey size (Lpreymin,mm)	$0.0115 * FL_{salmonid}$	Wankowski (1979)
Maximum prey size (Lpreymax,mm)	$0.452 * FL_{salmonid}$	Wankowski (1979), Hayes (2000)

### *Environmental variables*

When processing, MORPH follows a hierarchical order of parameters; at the start of each time step the global variables are first initialised then followed by patch and forager variables. Once defined, the environmental parameters of a patch are constant for the entire duration of the timestep. Invertebrate prey resource densities do not experience depletion from forager consumption on the assumption high chalk stream productivity (Wright et al. 2002) means that invertebrate drift densities are continuously replenished from invertebrate populations living in the benthos.

### *Forager processing and scheduling*

Foragers are scheduled in order of age and older foragers are processed first whilst the order of foragers within same age class is random; salmonid dominance is size dependent requiring a 30% size advantage to have priority over territory establishment (Johnsson et al. 1999). At the moment of immigration or entry into the model (time step = 1), foragers are able to occupy any patch within the stretch they first enter with the specific patch selected based on their fitness measure. At subsequent time steps, forager patch movement is limited to the patch it currently occupies and to patches one patch distance away upstream or downstream (i.e. forager move distance is limited to one patch distance up or downstream per hour). Foragers occupying one patch will influence the remaining area available for feeding by foragers that are yet to be processed. The area a forager occupies is defined by its territory size and there is a positive relationship between territory size and age (Grant & Kramer 1990).

During a time step, foragers can select between two behaviours: 'feeding' or 'resting'. A drift-feeding submodel that is dependent on both forager and patch environment variables determines the amount of drift consumed by a forager (Hayes *et al* 2000). Each activity has a 'swimming cost' associated with it and is a function of the speed they are swimming at as well as forager parameters and other environmental parameters. Foragers only

consume food when ‘feeding’ and swim at patch velocity. When resting, the speed at which fish swim at is reduced to 30% of patch velocity (following the assumptions made by Railsback & Harvey (2002)). Energy from the food consumed undergoes energy loss through imperfect assimilation efficiency, excretion losses and bioenergetic costs of digestion, standard metabolisms and swimming costs. This energy budget is converted into growth (positive or negative) by dividing net energy by specific energy content for salmonids. Forager consumption is maximally limited with the threshold defined by bioenergetic studies on brown trout growth under conditions of maximum and minimum food rations (Elliott 1975, 1976). Foragers can only ‘feed’ up until this limit and once reached foragers spend the remaining timestep ‘resting’. The bodymass of each fish is calculated and updated every timestep.

### *3.2.2.2 Design concept*

#### *Basic principles*

MORPH is constructed along the principles outlined in optimal foraging theory (Stillman 2008). Foragers select behaviours to achieve a user defined ‘fitness’ measure. The incorporation of growth and predation risk into this measure will lead foragers to distribute and grow accordingly within the virtual environment. The model is parameterised using published salmonid feeding models and bioenergetic equations.

#### *Emergence*

The model does not explicitly define i) the spatial patterns of distribution at the level of stretch (with the exception at the start of the simulation, Timestep=1, where the stretch population is defined to reflect observed distributions of fish at the start of the study period), ii) the patch an individual should occupy nor iii) the specific growth rates of foragers. Distribution patterns emerge during model simulations and these arise from the adaptive behaviours of individual foragers. Specific growth rates are

derived using a bioenergetic submodel but the inputs into this submodel are dependent on the forager behaviour, its traits and habitat characteristics. The growth rates for each fish emerge from these interactions. The initial macrohabitat distribution is defined but not the specific patch within the stretch they must occupy and this is constant across model simulations with no restrictions on forager movement between stretches at subsequent timesteps. As foragers move within the virtual environment, the distribution patterns at the macrohabitat (stretch) and mesohabitat (patch) scales will emerge.

#### *Adaptation and fitness*

Forager adaptive behaviours are 1) the ability to move between patches and 2) the proportion in a timestep spent either feeding or resting. Movement decisions are derived from selecting from the patch that returns the highest fitness measure.

#### *Objectives*

The main priority of foragers is to grow. The primary growth period for salmonids in chalk streams is in the more productive, warmer summer months and fish need to make the most of this period prior to the onset of more testing conditions during the winter months (Cunjak & Power 1987; Hunt 1969). The amount of forager growth is dependent on its net energy intake and is a function of the environmental conditions of the patch (e.g. resource density, water velocity and depth), forager variables (e.g. drift-feeding capture window) and the presence of other individuals within the patch (competition for space) (Hayes et al. 2000). A forager may only successfully feed if there is sufficient space remaining to establish a territory (Grant et al. 1998). Foragers can occupy a patch even if it cannot establish a territory to feed but cannot feed and still incur relevant bioenergetic costs. If a forager can successfully feed at a rate that reaches the theoretical maximum for that timestep, it will then consider the risk of predation in that patch.

### *Learning*

This model does not explicitly contain any forager ‘learning’. Foragers are provided with full awareness of parameters and variables from the start.

### *Prediction*

Foragers only ‘predict’ into the future at the start of a new timestep and select the behaviour with the highest fitness value. They do not project future fitness or growth beyond the current timestep.

### *Sensing*

Foragers have complete knowledge of the state variables of the patches they currently occupy as well as patches one patch distance upstream/downstream. Additionally, they have complete awareness of their forager variables and are aware of the location of larger foragers within a patch and can calculate the remaining territory area available (i.e. if the remaining space is sufficiently large enough for the forager to set up a territory to feed).

### *Interaction*

Foragers compete for the resource of space, as there is a requirement for establishing a territory in order to feed (Grant & Kramer 1990; Grant et al. 1998). The occupation of a patch by a forager decreases the amount of space remaining available for feeding by other foragers and patch space is a finite resource. Foragers processed first within each time step have priority over establishing territory and foragers do not compete directly for food resources once territories are already established. Foragers also interact with each other when assessing the predation risk of a patch - a function of predator density and the number of foragers within a patch.



### *Stochasticity*

At model initialisation, a forager's starting biomass is drawn from a normal distribution with the mean and standard deviation derived from recorded weights of corresponding foragers during fieldwork (i.e. forager type; see chapter 2, Figure 2.8, Figure 2.9, Figure 2.10). A stochastic process is also used to decide the processing order of foragers within the same age class. Finally, a forager will randomly decide between patches if all the patches available return the exact same measure of fitness.

### *Collectives*

A forager in the model is representative of a single individual forager.

### *Observation*

MORPH saves at user-specified timesteps, all global, patch and forager variables as well as additional diet parameter as outlined in Stillman (2008). To ensure comparable compatibility, the timesteps used for analysis correspond with the timesteps that fieldwork surveys were performed at the field site.

## *3.2.2.3 Details*

### *Initialisation*

The model environment (global and patch entities) is initialised at the start of a model and external files pertaining to the environmental variables are called in (Table 3.2 and Table 3.3). A total of 410 foragers split across 27 forager types (3 forager classes) are initialised and each forager has its starting biomass drawn from a defined normal distribution specific to its forager type (Table 3.4). A forager's starting location is defined at the level of the stretch and the forager decides the patch it first enters.

### *Input data*

Environment variables can be dynamic during a model simulation but do not differ between model simulations unless during parameter manipulation

during simulations. These are called into the model through the use of external files detailing the value of that variable for that time step. The environment variables are not affected by foragers. Except for model initialisation, all changes to forager variables are a result of interactions between forager and the environment or with other foragers.

#### *Environmental submodels*

A simulation run is representative of 85 days and each day is divided into 24 time steps with each time step representative of an hour. The discharge conditions for the first 68 days are of natural flow whilst the remaining 17 days are under a severely reduced flow. Water temperature for a timestep was measured *in situ* in the field and hourly temperature readings are averaged to give mean day temperatures. Timesteps are distinguished as either day or night with the first timestep of the day the same hour that dawn breaks for that particular day and the same with sunset and night-time. All of these variables are read from files based on recorded data (see chapter 2 for detailed description).

#### *Depth and velocity*

Patch depth and velocity were calculated for each timestep using a quasi 1-D hydrological model (see chapter 2). Depth and velocity were given as mean values for the timesteps.

#### *Resource (invertebrate) density*

Drift net samples are used to characterise the size structure of invertebrate drift in each stretch (see chapter 2). Aquatic and terrestrial invertebrate densities are classified into 5 length classes (1-3; 3-5; 5-7; 7-9; 9-12 mm) to give a total of ten resource categories (5 classes each for aquatic and terrestrial invertebrates). The total drift density per stretch are estimates from a function between 1) drift densities estimated from samples collected from drift nets and 2) drift densities estimated from densities of benthic invertebrates from surber nets. This is to overcome known biases in

sampling drift densities using a drift net methodology that arise from the clogging of the net and complex flow around the mouth of the net (Faulkner & Copp 2001). An assumption is made that whilst sampling errors affect estimates of total drift densities, the size structure of the invertebrate drift is representatively captured; sampling biases in collection are assumed constant for all invertebrate drift classifications (i.e. invertebrate size and origin) with the sampling error only affecting the estimate of total drift densities.

Estimates of drift density are possible by recording benthos invertebrate data as the majority of invertebrate drift that is aquatic in origin are drifting benthos; at any moment in time, a percentage of the benthos invertebrate population has entered the water column or are ‘drifting’ (Brittain & Eikeland 1988; Hemsworth & Brookers 1979). This percentage of ‘spontaneous benthos drift’, or SBD, has been measured at 0.004 to 0.13% of the total benthos population (Hemsworth & Brookers 1979; Williams 1980) and the latter is due to the known productivity of chalk streams. Drift density is calculated as:

$$DD_{benthos_i} = \frac{SBD * BD_i * SA_i}{\sum(PA_i * PD_i)}$$

Where  $i$  is the stretch; DD is drift density from benthos samples (number.m<sup>-3</sup>); SBD is the spontaneous benthos drift (fixed at 0.0013 from Hemsworth & Brookers 1979); BD is the density of benthos invertebrates estimated from surber nets; SA is stretch area (m<sup>2</sup>); PA is the area of patches belonging to that stretch; PD is mean depth of all patches in the stretch on the day of sampling.

To quantify the difference between estimates of invertebrate drift densities from drift net samples versus estimates from benthic densities collected from surber nets, a ‘correction coefficient’ (CC) per sample event is calculated. The CC is the ratio between estimated drift densities from

benthos data ( $DD_{benthos}$ ) and the (biased) estimated drift densities from drift net collections ( $DD_{drift}$ ) and is calculated as:

$$CC_i = \frac{DD_{benthos_i}}{DD_{drift_i}}$$

Where  $CC$ =correction coefficient,  $i$  = sample,  $DD_{benthos}$  = estimated drift densities from benthos density,  $DD_{drift}$  = estimated drift densities from drift net samples.

There was no significant temporal trend in  $CC$  (ANOVA,  $p>0.05$ ) (i.e. the mean  $CC$  did not differ sample dates) but significant differences were observed between samples collected from different stretches (ANOVA,  $p<0.05$ ) so a spatial difference between  $CC$  but not a temporal one is observed. The  $CC$  for each sample date for each stretch is calculated and used to calculate drift densities for each resource category by multiplying the drift densities estimated from drift nets (size structure of invertebrate drift) with the respective mean  $CC$  for that specific stretch.

Drift densities for each resource category were calculated for each stretch for each time step. Samples were taken at three times during a day (dawn, mid-day and dusk) and are used as reference points with a linear interpolation between the two closest points used to fit the densities at timesteps during sample reference points. Densities at night are assumed to be the same as dusk densities (Neale et al. 2008). No significant trend for densities of terrestrial drift was observed (Kruskal-Wallis,  $p>0.05$ ) and thus assumed to be constant throughout the day but zero at night. A linear relationship is also used to estimate respective resource densities between sampling dates.

Average dry mass (g) and energy density ( $KJ.g^{-1}$ ) for each resource category was calculated using length-mass and mass-energy relationships (Benke et al. 1999; Ganihar 1997; Sabo et al. 2002; Cummins & Wuycheck 1971) and

provided a means to convert drift densities into energy. Larger invertebrates provide more energy per item than small invertebrates.

### *Predator densities*

In chalk stream environments, European pike (*Esox lucius*) are the main aquatic predators of salmonids (Mann 1982). Data on pike densities were collected at the same time as salmonid data and pike are classified into two categories (fork length < 218mm; fork length > 218mm; see chapter 2). Densities for each pike size category in the model are an overall mean of estimated densities from fish population surveys (see chapter 2). Predator densities are modelled as an environmental parameter at the scale of the stretch (no. of pike.m<sup>2</sup>) with each patch within a stretch having the same pike density. Estimates of the max prey body depth (or gape size) for the two pike size categories (Nilsson & Bronmark 2000) along with estimates of salmonid body depth allowed for the identification of the forager class categories in the model that are vulnerable to predator groups (Table 3.4).

Table 3.4 The age class of foragers vulnerable to different predator sizes

Pike age	FL (mm)	Max prey body depth (mm)	Salmonid age class vulnerable to predation
Juvenile	<218	28.34	Young-of-year (YoY)
Adult	>396	51.48	Young-of-year (YoY) and one year old (1+)

### *Forager Types*

Each forager is classified at two levels; i) *Forager Class* defines the species and age of the forager and ii) *Forager Type* has additional details about the stretch the forager must start at, the bodymass distribution for that forager class for its starting stretch and if it was implanted with a PIT tag. These forager types allow for a more accurate representation of observed population of salmonids at the start of the fieldwork period and help in model processing.

The permutations of different characteristics lead to the creation of 84 forager types in the model but not all are used (See Table 3.3). Not all forager types need to exist for a simulation to occur and the number of foragers and forager types are representative of field observations (but can be manipulated by the user). The range of forager types presents an advantage as it allows for the testing of the effect that different population structures (e.g. stocking or removal events) might have on population patterns.

#### *Population characteristics*

The total number of individuals of any particular forager type is derived from population estimates calculated from the first electric fishing survey. Age is calculated from scale samples and length-weight relationships and population characteristics recorded. Starting forager bodymass is drawn from a normal distribution of observed body mass for each respective forager type (see chapter 2).

#### *Territory size*

Forager territory size has been measured as a function of forager fork length (Keeley 2000; Grant & Kramer 1990). In this model, territory size is a fixed value and is estimated for each age class of individuals (0+, 1+). A weighted mean fork length is derived from observed measurements of fish caught throughout the field season.

### *Forager bioenergetics*

Elliott (1975, 1976a, 1976b) carried out a series of extensive experimental-based investigations into the bioenergetics of brown trout. All of Elliott's bioenergetic equations are provided using units of measurement in the form of calories day<sup>-1</sup> but is transformed into KJ day<sup>-1</sup> in this model (1 calorie = 4.1868 KJ). Net energy intake is calculated by:

$$C = F + U + R + \Delta B$$

Where C = energy consumed; F = energy associated with faeces; U = energy associated with excretory products; R = energy lost through respiration processes;  $\Delta B$  = change in biomass.

### *Energy consumed by an individual forager*

The amount of food consumed by a fish is defined by submodel describing the drift-feeding behaviour of salmonids (Railsback & Harvey 2002). This submodel accounts for i) the availability of prey (invertebrate drift), ii) the detection of prey items by the fish and iii) the probability of a success capture and consumption of a prey item.

### *The availability and access to patch resources - diet*

Foragers can only access a section of the total invertebrate drift within a patch and is termed 'forager diet' and this parameter defines which of the invertebrate resources present in the patch a forager can feed from. A forager's diet is determined by the minimum and maximum size of invertebrates a forager can consume defined by its gill raker spacing from Wankowski (1979) and Hayes et al. (2000). If the threshold size falls within a size category, the entire size resource is available for consumption by the forager.

#### *The capture of drifting invertebrates*

Salmonid drift-feeding behaviour involves the fish taking a position within an area of flowing water (i.e. the 'run' section of a patch) and swimming at a speed constant to the velocity of the water so as to be in a stationery position (Railsback & Harvey 2002). The fish will then feed off drifting invertebrates within the flowing water but this is limited to items that enter and pass through a 'capture window' (Hayes et al. 2000). The size of the capture window is dependent on the distance a forager will identify a potential item of invertebrate drift or its 'reaction distance' (RD) (see Table 3.3). The rectangular capture window (area) is a function of an individual's reaction distance and the depth of water in the patch it is occupying as the capture window (vertical distance) limited by the depth of water (i.e. an individual's RD may exceed the depth of water but it cannot feed out of water) (Table 3.3). In this model, salmonids are diurnal visual feeders (Hayes et al. 2000) and so RD at night = 0. Not all invertebrates that enter a forager's capture window are successfully captured with the probability of a successful capture (capture probability) having an inverse relationship with water velocity (see Table 3.3).

#### *The capture rate Handling time of capture invertebrates*

The time spent handling a single food item is a function of the time taken for the forager to swim to a detected food item and return to its position (Hayes et al. 2000, see Table 3.3). The amount of food captured by a forager in a single timestep is determined by the i) capture probability, ii) rate of encounter, iii) prey density and iv) handling time (Hughes et al. 2003 see Table 3.3).



### *Temperature thresholds*

Once consumed, prey items must be digested and assimilated with salmonid bioenergetics closely linked with individual size and water temperature. The equations used to estimate salmonid bioenergetics are temperature dependent. The temperature thresholds and parameters for the equation in Table 3.3 used for these thresholds are shown in Table 3.5.

Table 3.5. Mean and standard deviations of estimated normal distributions for the parameters of the equations in Table 3.3. used to estimate  $C_{max}$ ,  $R_{max}$ ,  $R_{standard}$  within temperature bonds and the assimilation efficiency used to investigate parameter bias. Mean and standard deviations are calculated from confidence intervals and observed ranges from Elliott (1976a & 1976b).

Parameter	Temperature (°C)	Mean $\pm$ s.d.	
		$b_1$	$b_2$
$C_{max}$	6.6-13.3	$0.759 \pm 0.01173$	$0.171 \pm 0.00612$
	13.3-17.8	$0.767 \pm 0.02092$	$0.126 \pm 0.01582$
	17.8-21.7	$0.753 \pm 0.04388$	$-0.662 \pm 0.02755$
$R_{max}$	3.8-17.8	$0.770 \pm 0.01296$	$0.204 \pm 0.00201$
	17.8-19.5	$0.757 \pm 0.01061$	$-0.663 \pm 0.02755$
$R_{standard}$	3.8-7.1	$0.734 \pm 0.01311$	$0.731 \pm 0.01122$
	7.1-19.5	$0.192 \pm 0.01250$	$0.0938 \pm 0.00207$
Assimilation efficiency	all	$69\% \pm 1\%$	

### *Maximum consumption rate ( $C_{max}$ )*

The maximum consumption rate of brown trout is used within the model to explicitly state the maximum energy intake allowed by an individual. Following the approach by Hayes et al. (2000), forager consumption only occurs during daylight hours, the  $C_{max}$  equation is further transformed (after  $\text{KJ hr}^{-1}$ ) by dividing the total number of daylight hours in that day:

$$C_{max \cdot timestep_{daylight}} = 4.1868/1000 * C_{max} / \text{DaylightTimeStep}$$

Where  $C_{max \cdot timestep_{daylight}}$  is the maximum amount of energy consumed by a forager per each daylight timestep in that day (KJ);  $C_{max}$  is the maximum daily energy consumption for a forager per day (calories)';  
DaylightTimeStep is the hours of daylight in that day.

#### *Faeces ( $F_{max}$ ) and Excretion ( $U_{max}$ )*

The energy loss through faeces and urea is non-physiologically useful and is not available for respiration or growth. The energetic values for  $F_{max}$  and  $U_{max}$  are made available, however, in Elliott (1976b) the percentage of energy lost through  $F_{max}$  and  $U_{max}$  is fairly constant even for different sized individuals under  $C_{max}$  conditions even under a range of temperatures;  $F_{max} + U_{max}$  remained between 30-32% of total energy ingested for the temperature range of 3.8-19.5°C from Table 3 in Elliott (1976). In the model,  $F_{max}$  and  $U_{max}$  are accounted for through a fixed 31% loss by assuming a 69% assimilation efficiency of energy consumed made available for respiration and growth. Setting a fixed 31% lost to  $F_{max}$  and  $U_{max}$  works under the assumption that the individual is consuming at a rate equivalent to  $C_{max}$ . Following the approach by Hayes et al. (2000) and to to minimise model complexity, the assumption that  $C_{actual} = C_{max}$  was used and  $F_{max} + U_{max} = 31\%$  of energy consumed.

### *Respiration (R<sub>max</sub>)*

The total energy represented by respiration processes consists of three components:

$$R_{\max} = R_{\text{standard}} + R_{\text{digestion}} + R_{\text{activity}}$$

Where  $R_{\text{standard}}$  is respiration by ‘standard’ metabolism processes excluding digestion costs;  $R_{\text{digestion}}$  is the energetic cost associated with digestion;  $R_{\text{activity}}$  is the cost of activity.

In the experimental setup in Elliott (1976) individuals were exposed to very minimal water current and it was concluded by Hayes et al. (2000) and even in Elliott (1976) that overall fish activity was very low therefore  $R_{\text{activity}}$  can be considered as negligible or null in the equation of  $R_{\max}$ . Equations for calculating  $R_{\max}$  and  $R_{\text{standard}}$  are provided and  $R_{\text{digestion}}$  is calculated as:

$$R_{\text{digestion}} = R_{\max} - R_{\text{standard}}$$

Where  $R_{\text{standard}}$  is respiration by ‘standard’ metabolism processes excluding digestion costs;  $R_{\text{digestion}}$  is the energetic cost associated with digestion

As with  $F_{\max}$  and  $U_{\max}$ , the cost of  $R_{\text{digestion}}$  is closely linked with the amount of food an individual consumes. Elliott’s (1976) estimation of  $R_{\text{digestion}}$  is proportional to amount of food consumed in relation to the maximum rate of food consumed. The assumption used in this model is that a forager’s  $R_{\text{digestion}}$  is always at the maximum. Respiration is modelled as occurring at every timestep (i.e. not dependent on daylight) and energy associated with digestive respiration processes in the model is equal to  $R_{\text{digestion}}$  (KJ.day<sup>-1</sup>) divided by 24.

### *Swimming costs (SC)*

The respiration cost associated with swimming activity is interpreted differently from 'Ractivity' in Elliott (1976b) because brown trout were not subject to significant flow velocity in their experiments and time (and energy) spent swimming was negligible (Hayes et al. 2000). Hayes et al. (2000) defined its own equation to estimate forager swimming cost (or activity), however their formula combines standard metabolism ( $R_{\text{standard}}$ ) with the cost of swimming at a certain velocity (SC). The definition of SC in this salmonid IBM is different as it is the energetic cost associated just with swimming activity (i.e. it does not include cost associated with standard metabolism). SC in this model is defined by removing  $R_{\text{standard}}$  from the formula for 'SC' in Hayes et al. (2000):

$$\text{Swimming Cost}_{(\text{this model})} = \text{Swimming Cost}_{(\text{Hayes et al. 2000})} - R_{\text{standard}}$$

When feeding, a forager swims at 100% of patch velocity ( $SC_{\text{feeding}}$ ). When not feeding, following Harvey & Railsback's (2009), foragers swim at 30% of patch velocity.

*The bioenergetic cost of behaviours within the model*

Within a timestep, individuals are either i) feeding or ii) resting. When feeding, individuals are consuming and respiring but whilst resting, individuals are not consuming but still respiring.

The bioenergetic cost when feeding is equal to:

$$\text{Respiration}_{\text{feeding}} = R_{\text{standard}} + R_{\text{digestion}} + SC_{\text{feeding}}$$

and the bioenergetic cost when resting is equal to:

$$\text{Respiration}_{\text{resting}} = R_{\text{standard}} + R_{\text{digestion}} + SC_{\text{resting}}$$

where  $\text{Respiration}_{\text{feeding}}$  is the energy spent feeding;  $R_{\text{standard}}$  is the energy spent on standard metabolism;  $R_{\text{digestion}}$  is the energy spent on digestion processes;  $SC_{\text{feeding}}$  is the energy spent through swimming at speeds associated with resting

Total respiration per time step is calculated at:

$$\text{Total respiration}_{\text{timestep}} = a * \text{Respiration}_{\text{feeding}} + (1-a) * \text{Respiration}_{\text{resting}}$$

where  $a$  is the proportion of a timestep a forager spends feeding

### *Fitness rule*

Patch choice decisions followed a fitness-maximising rule that placed a premium on growth rates. It is calculated based on the following assumptions:

- If rate of consumption achieves  $C_{max}$ ; predation risk is considered and select behaviour that minimises predation risk.
- If rate of consumption does not achieve  $C_{max}$ ; predation risk is unaccounted for and select behaviour that maximises consumption

It is assumed that predation risk is equal for all individuals vulnerable to the respective predator sizes. Predation risk is calculated at the patch level as:

$$PR_i = \frac{PD_i}{VF_i}$$

Where PR is predation risk, PD is predator density, VF is number of foragers vulnerable to predation and  $i$  is the patch number.

### 3.2.3 Model Analysis

#### *Specific growth rates (SGR)*

The growth rates of foragers are calculated as specific growth rates or the percentage change in body mass per day (%bodymass.day<sup>-1</sup>). This is expressed as:

$$SGR = \frac{\ln(W_{salmonid\ t_n}) - \ln(W_{salmonid\ t_0})}{t_n - t_0} * 100$$

Where SGR is the specific growth rate,  $W_{salmonid\ t_0}$  is the initial mass at tagging ( $t_0$ ) and  $W_{salmonid\ t_n}$  is the mass at recapture and  $t_n - t_0$  is the number of days between recapture.

#### *Forager population distribution at the stretch level (macrohabitat)*

The ‘macrohabitat forager distribution’ is a measure of the distribution of foragers in the model environment and is expressed as the forager per stretch as a proportion of the total population. Poor depletion during fieldwork data collection or low probability of capture, will lead to high variance when estimating stretch density. If probability of capture < 20%, the stretch was omitted from analysis (see chapter 2).

Macrohabitat distribution is measured as relative proportions per stretch and is calculated as:

$$Proportion_{stretch,i} = \frac{no.individuals\ in\ stretch_i}{total\ no.individuals\ in\ stretch_{all}}$$

Where  $i$  is the stretch being analysed and  $all$  is all the stretches considered in the analysis (stretches with probability of capture < 20% were removed from analysis – see chapter 2).

#### *Forager population distribution at the patch level (mesohabitat)*

The distribution of tagged salmonids during fieldwork was recorded by tracking tagged individuals with a portable PIT tag tracking antenna (see

Chapter 2 and Cucherrouset *et. al* 2010). The time and patch location of tagged individuals provided patch patterns of forager distribution at specific time steps. The patches that are occupied by foragers in the model at the corresponding timesteps are compared to the observed pattern of occupied patches in the natural system.

#### *Measuring model variation*

To measure the effect of intrinsic model variation on predicted patterns, 100 replicate model simulations were run on the same parameterset and the variation between predicted growth rates of YoY Atlantic salmon, YoY brown trout and 1+ brown trout between simulations was calculated. 95% confidence intervals of estimated specific growth rates for each of the three forager types was first calculated using two model outputs selected at random from the hundred and this was repeated 1000 times to calculate the variation in mean growth rates a two replicate simulation investigation would generate. This process was repeated for three model simulations, then four etc., up to a hundred to determine the resolution increasing the number of model runs on the confidence in model predictions. The number of replicates used in future model analysis was determined at the plateau phase where increasing the number of replicates did not yield significantly smaller confidence intervals.

#### *Comparing predicted and observed patterns*

The specific growth rates of foragers were calculated for two environmental periods of discharge regimes; natural flow and reduced flow. For these two periods, the mean SGR for YoY salmon, YoY trout and 1+ trout were compared against mean SGR from field-collected data by means of Welch's two samples t-test.

#### *Sensitivity analysis*

A sensitivity analysis was performed for each parameter not empirically measured during fieldwork. Each parameter value was modified by  $\pm 25\%$



and model simulations were independently run for individual parameters. The deviation of these forager SGRs from the SGR calculated under the ‘baseline’ (i.e. unmodified) model was used to identify the most sensitive parameters of the model.

#### *Bias in parameter estimation*

After identifying the most sensitive parameters, the implications uncertainty in parameters had on predicted forager SGR was analysed. The confidence intervals published along parameter estimates of the top four parameters the model is most sensitive to was used to define the distribution of parameter estimates (i.e. a normal distribution of possible estimates for that parameter). 100 parameter estimates were drawn from this distribution and five replicate simulations were performed for each parameter estimate. Where there was more than one distribution involved in the estimation of one parameter (e.g.  $C_{\max}$  has two possible distributions; one for  $b_1$  and one for  $b_2$ , Table 3.5), the numbers drawn for each distribution was sorted by size the pair used in the final parameter estimate for model simulation.

### 3.3 Results

#### *3.3.1 The effect of increasing the number of model simulations on confidence intervals of forager growth rates*

Analysis of the variation in forager specific growth rates (SGR, % bodymass day<sup>-1</sup>) produced by repeated simulations of the same parameter set indicated that an increase in the number of replicate simulations produced a more accurate prediction of mean model predictions (Figure 3.1) and this is seen in the SGR of all three forager classes. The number of replicates used in model analysis from thus onwards was set at five model replicates as a trade-off between confidence in parameter estimate and modelling time. The 95% confidence interval in predicted SGR for all foragers after five model replicates was calculated to be below 0.09% bodymass day<sup>-1</sup>.

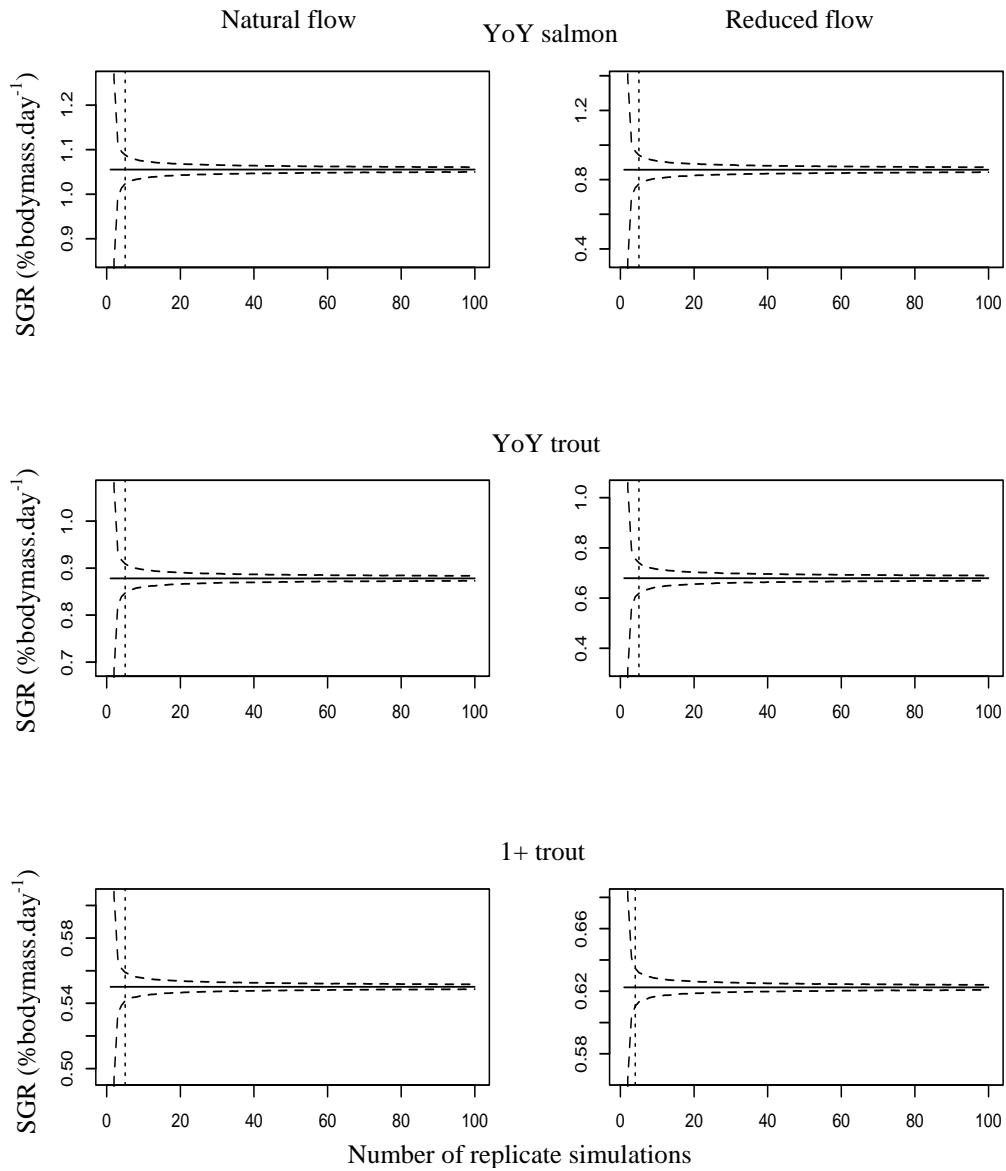


Figure 3.1 The relationship between the number of model replicates and the confidence in estimating the mean population specific growth rate in three forager classes; ‘young-of-year’ (YoY) or 0+ Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) and 1+ brown trout. Dashed lines indicate 95% confidence intervals of mean growth rate; solid line is the mean of the all hundred replicates; vertical dotted lines indicate five model replicates.

### *3.3.2 Predicted vs. observed specific growth rates (SGR)*

Overall, the predicted SGR of foragers in the forager classes (YoY Atlantic salmon, YoY trout and 1+ trout) show a good comparison with observed SGR of real foragers (Figure 3.2). Mean predicted SGRs always overestimated mean observed SGRs but nearly all are within the quartile range for the YoY salmonids over both flow periods; the exception were 1+ trout SGRs as these were consistently predicted at higher rates outside the quartile range. The SGR predicted for YoY Atlantic salmon for both the natural and reduced flow periods were not significantly different from observed rates of growth (t-test,  $p > 0.05$  for both). The predicted SGRs of YoY trout and 1+ trout for the two flow regimes were significantly different from observed growth rates (t-test,  $p < 0.05$ ).

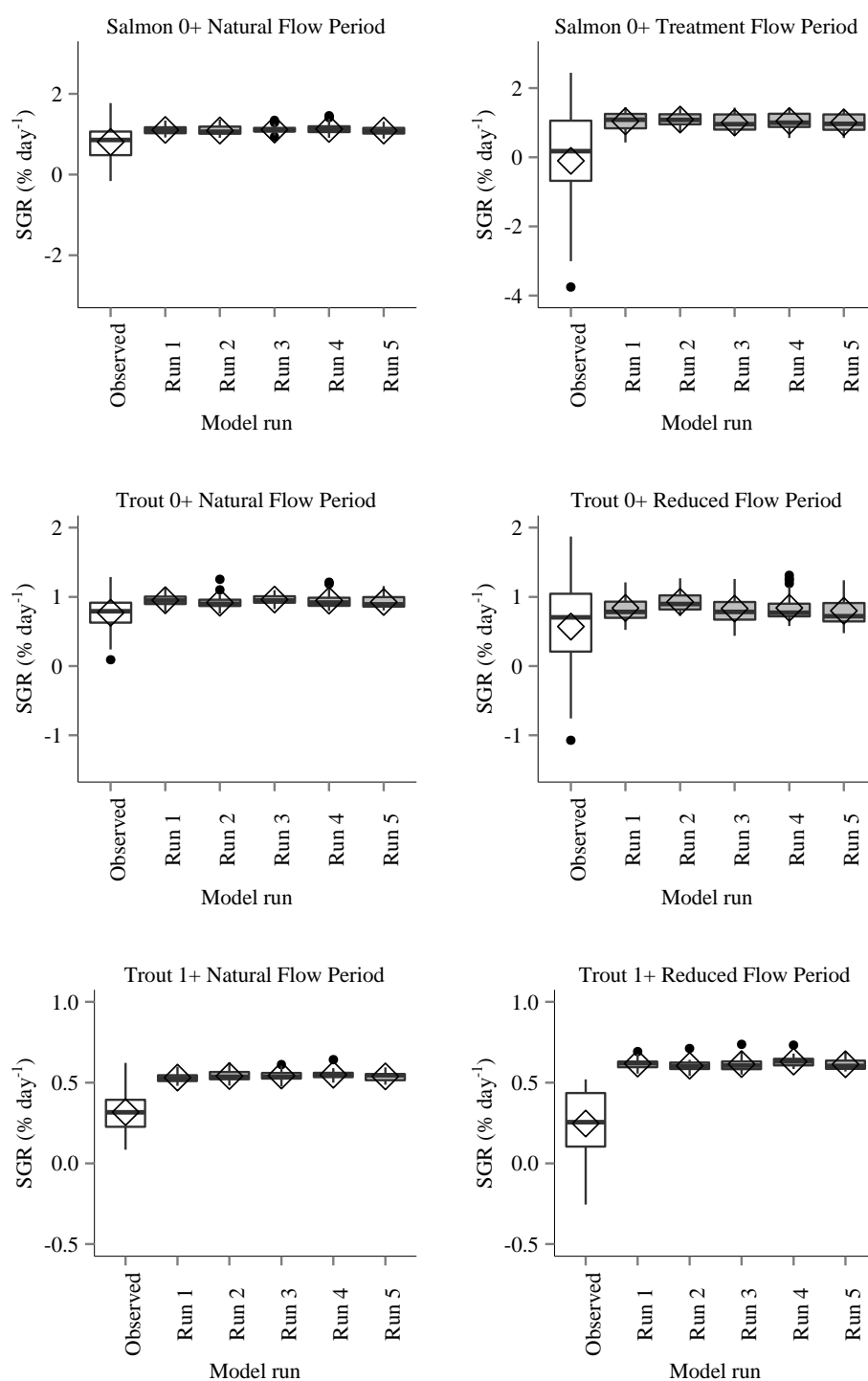


Figure 3.2 Observed and predicted population growth rates of young-of-year (YoY) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) and 1+ brown trout. Observed growth rates (white) were collected at a chalk stream study site over two flow regimes (natural and reduced; left and right columns respectively) with predicted growth rates (grey) from the salmonid individual based model (IBM). The environment in model simulations reflected the conditions at the study site. The diamond indicates mean SGR for each distribution.

### *3.3.3 Distribution at the stretch level*

The predicted distribution of foragers at the scale of the stretch proves a close fit with the observed patterns of forager densities in the chalk stream (Figure 3.3, Figure 3.4 and Figure 3.5). However model predictions underestimated the densities of stretch 4 for both YoY Atlantic salmon and brown trout but overestimated it for 1+ brown trout. It also underestimated the density of stretch 1 for 1+ trout foragers.

Figure 3.6 compares predicted and observed distributions as a function of each other. Statistical testing of a linear relationship between observed and predicted densities against perfect prediction (i.e. a linear model with y intercept = (0,0) and a gradient of 1) showed varying predictive power across forager types. The predicted stretch distribution of YoY salmon did not significantly differ from perfect prediction (linear regression intercept is not significantly different from (0,0), t-test,  $p > 0.05$  & linear regression gradient is not significantly different from 1, t-test,  $p > 0.05$ ). The predicted stretch distribution of YoY trout showed mixed results as whilst the slope did not significantly differ from perfect prediction, the intercept of the linear model did (intercept significantly different from (0,0), t-test,  $p < 0.05$  and gradient not significantly different from 1, t-test,  $p > 0.05$ ). The linear model of 1+ trout significantly differed from perfect prediction (intercept significantly different from (0,0), t-test,  $p < 0.05$  & gradient significantly different from 1, t-test,  $p > 0.05$ ), however, the slope of the linear model is positive indicating that the stretches that are predicted to have a higher density of foragers were observed to have a higher density of foragers.

### *3.3.4 Distribution at the patch level*

The model is best able to predict the patch distribution of YoY Atlantic salmon, correctly predicting, on average, 82.4% of all patches real YoY Atlantic salmon were recorded being in during fieldwork. The patch distribution of YoY and 1+ brown trout average was lower at 65% and 48.6% for respectively (Table 3.6).

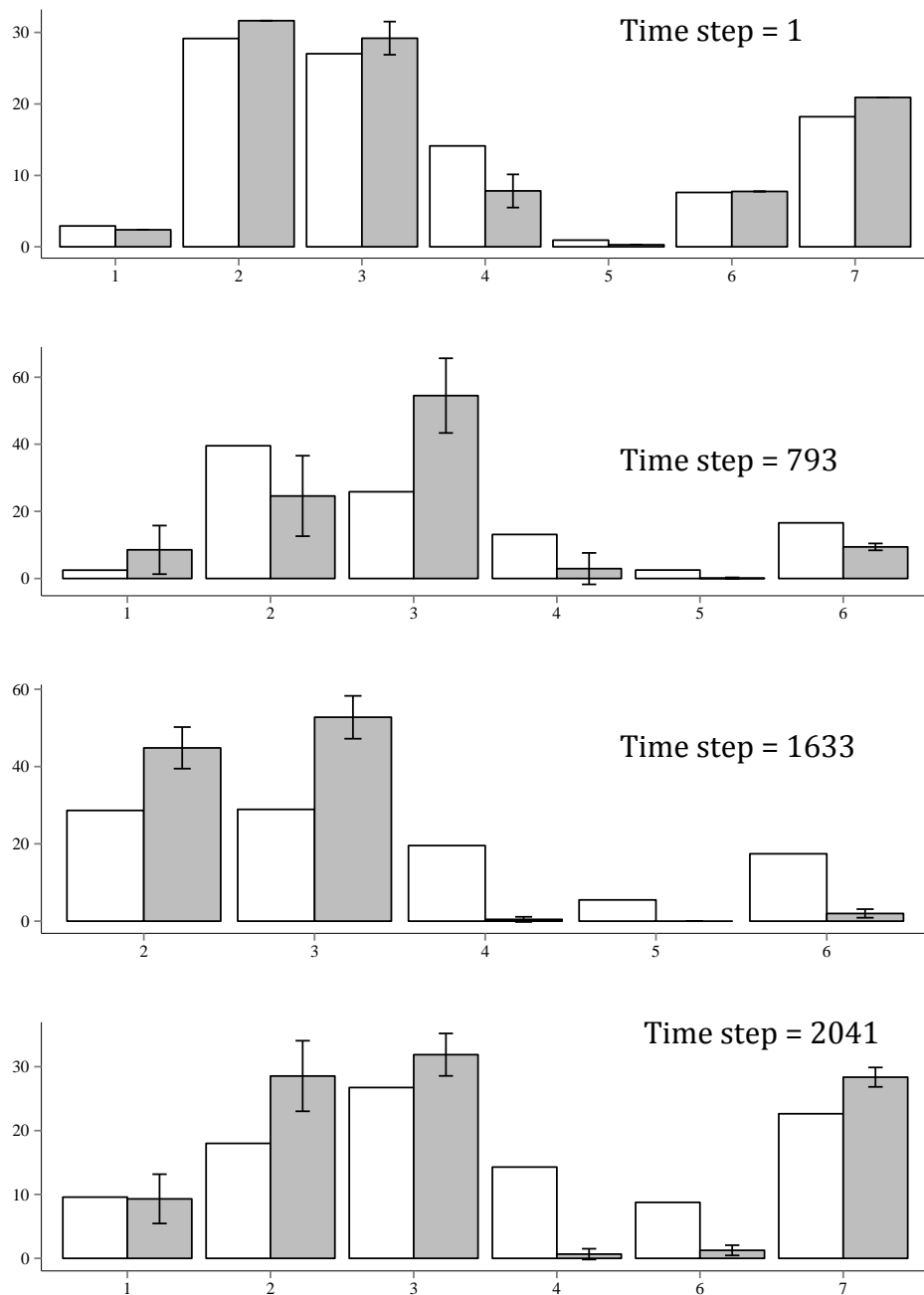


Figure 3.3 Comparing observed and predicted distributions of young-of-year (YoY) Atlantic salmon (*Salmo salar*) as relative proportions (% of total population) across the different stretches (1-7). Observed distributions are shown in white and distribution was measured by population depletion sampling (electric fishing). Model predicted distributions are shown in grey. Error bars indicate the standard deviation of 5 model replicates and the distribution of fish in the model were compared at timesteps that directly correspond with population sampling events carried out during the study period. Stretches were omitted from comparison if the confidence of population estimates from electric fishing sampling were low (i.e. due to poor depletion – see chapter 2).

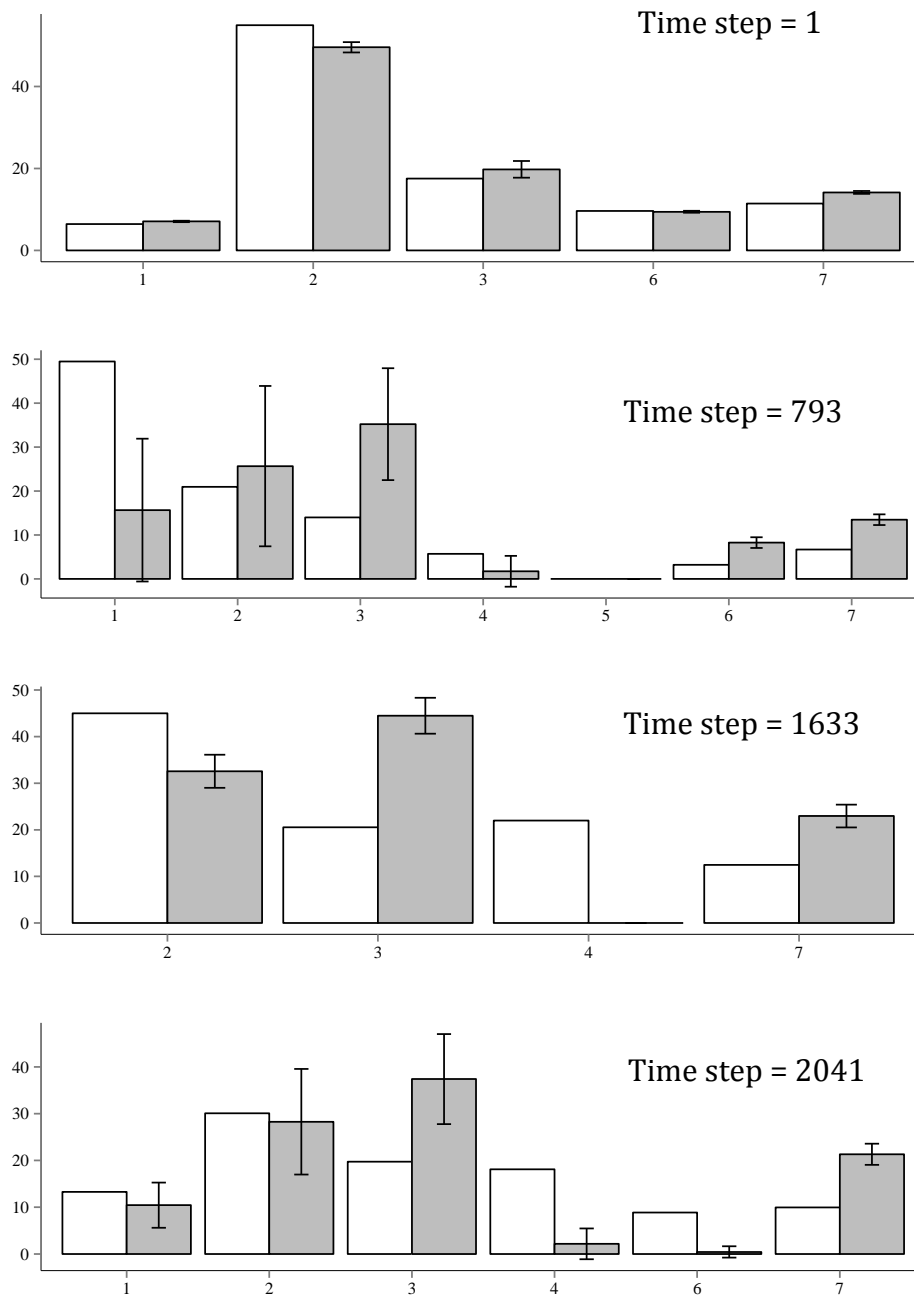


Figure 3.4 Comparing observed and predicted distributions of young-of-year (YoY) brown trout (*Salmo trutta*) as relative proportions (% of total population) across the different stretches (1-7). Observed distributions are shown in white and distribution was measured by electric fishing sampling events. Model predicted distributions are shown in grey. Error bars indicate the standard deviation of 5 model replicates and the distribution of fish in the model were compared at timesteps that directly correspond with population sampling events carried out during the study period. Stretches were omitted from comparison if the confidence of population estimates from electric fishing sampling were low (i.e. due to poor depletion – see chapter 2).



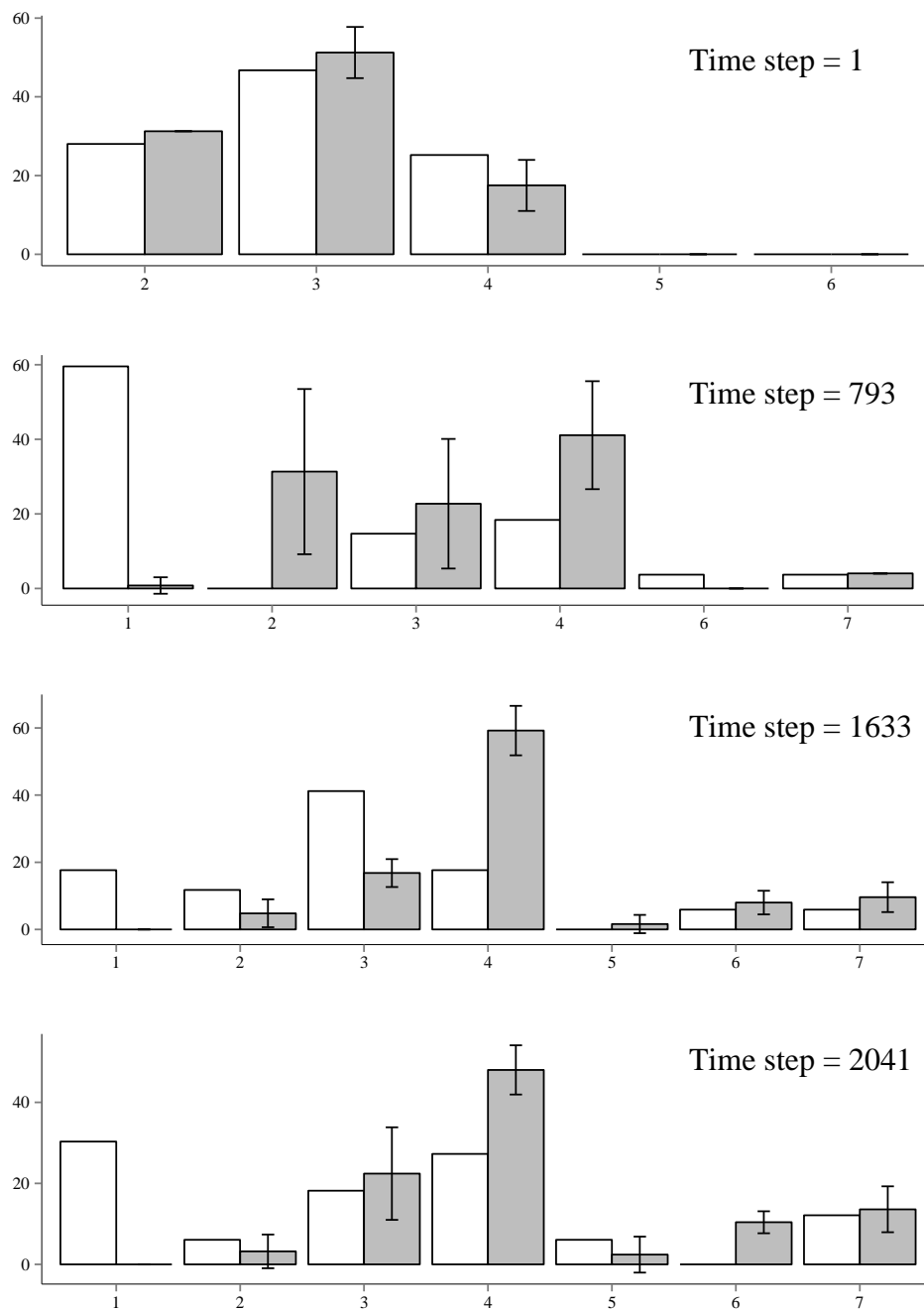


Figure 3.5 Comparing observed and predicted distributions of one-year-old (1+) brown trout (*Salmo trutta*) as relative proportions (% of total population) across the different stretches (1-7). Observed distributions are shown in white and distribution was measured by electric fishing sampling events. Model predicted distributions are shown in grey. Error bars indicate the standard deviation of 5 model replicates and the distribution of fish in the model were compared at timesteps that directly correspond with population sampling events carried out during the study period. Stretches were omitted from comparison if the confidence of population estimates from electric fishing sampling were low (i.e. due to poor depletion – see chapter 2).

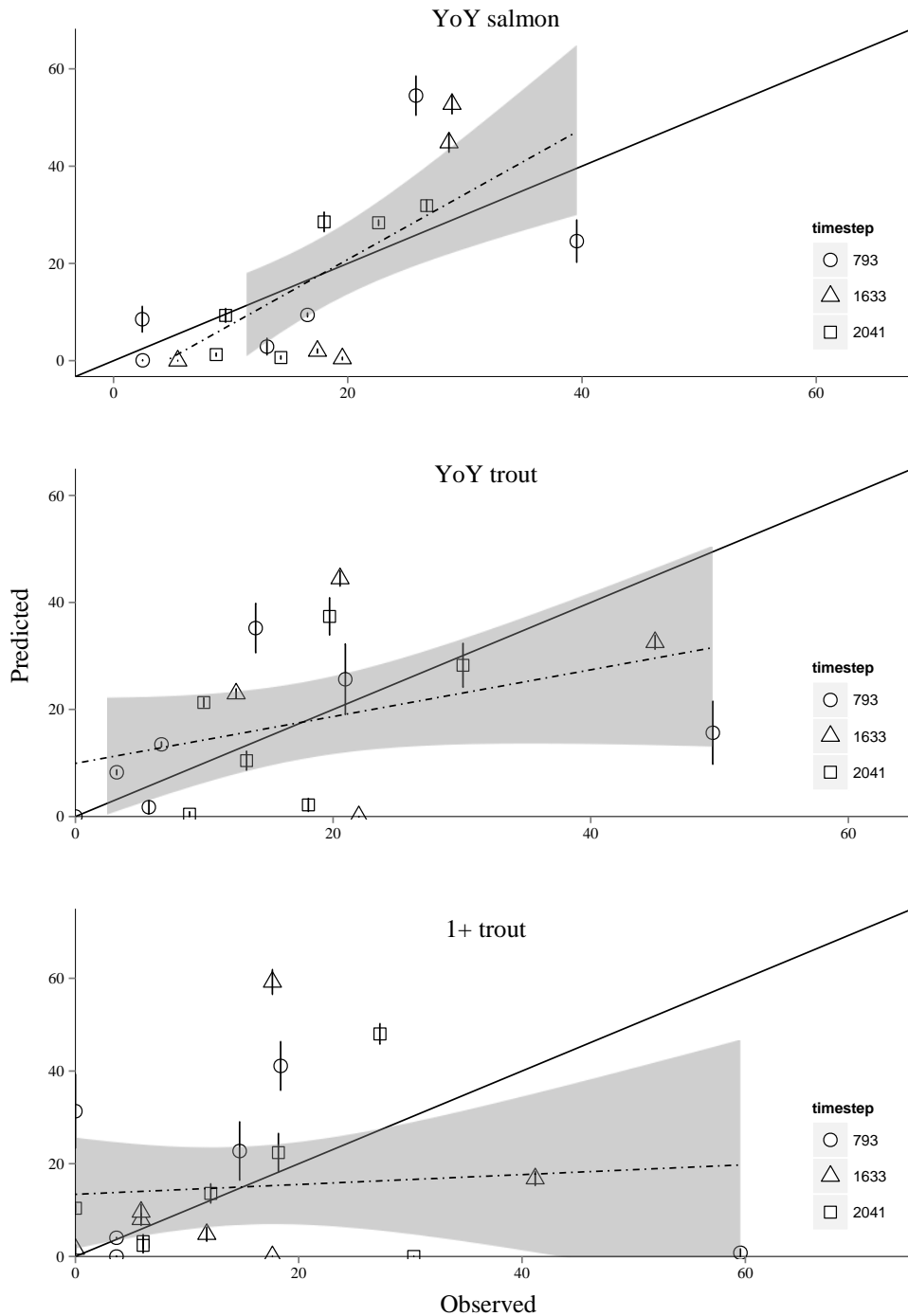


Figure 3.6 The ability of the model to accurately predict the distribution of fish at the scale of the stretch; predicted distributions are plotted against observed distributions. A linear regression model of the relationship is represented by the dotted line whilst the solid line represents a 1:1 ratio (perfect prediction). The shaded area shows the 95% confidence intervals for the regression line. The forager types are young-of-year (YoY) Atlantic salmon (*Salmo salar*), YoY brown trout (*Salmo trutta*) and year old (1+) brown trout (top, middle, bottom graphs respectively). The time steps are corresponding to the same timesteps of sampling events (electric fishing) performed on the observed fish population at the study site.

Table 3.6. The total number of correctly predicted patch occupancy by virtual ‘young-of-year’ (YoY) and one-year-old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in the salmonid IBM when compared with real fish in a chalk stream environment. Fish distributions were observed using portable passive-integrated transponder (PIT) tags to locate previously tagged fish in the field site. The number outside the brackets indicate the number of patches correctly predicted whilst the number in brackets indicate the total number of patches missed; the sum of the two is the total number of patches that forager class was observed to occupy during fieldwork in that timestep.

Forager Type	Timestep								
	295	335	631	1029	1588	1614	1774	1852	2014
Salmon 0+	12 (1)	9 (4)	9 (3)	9 (1)	11 (1)	14 (1)	13 (2)	16 (16)	14 (1)
Trout 0+	6 (2)	14 (14)	8 (2)	13 (13)	9 (3)	6 (6)	9 (4)	11 (4)	10 (6)
Trout 1+	6 (5)	2 (1)	2 (4)	4 (3)	3 (3)	1 (6)	3 (3)	4 (2)	4 (5)

### 3.3.5 Sensitivity analysis

The sensitivity analysis of model parameters derived from published literature indicates a high variance in their effect on model predicted forager growth rates. Parameters associated with the behavioural drift-feeding submodel (i.e. *handling time*, *reaction distance* etc.) had little effect on predicted SGR. Resource parameters like resource energetics and density had a higher impact but this was still minimal when compared to forager-specific bioenergetic parameters (Figure 3.7, Figure 3.8 and Figure 3.9). Forager specific growth rate was most sensitive to the maximum consumption rate of foragers with YoY salmon showing the greatest sensitivity of the forager types. The order of sensitive parameters also showed a high concordance between all three forager types except for respiration max and resting metabolic rate that had their positions reversed for 1+ trout.

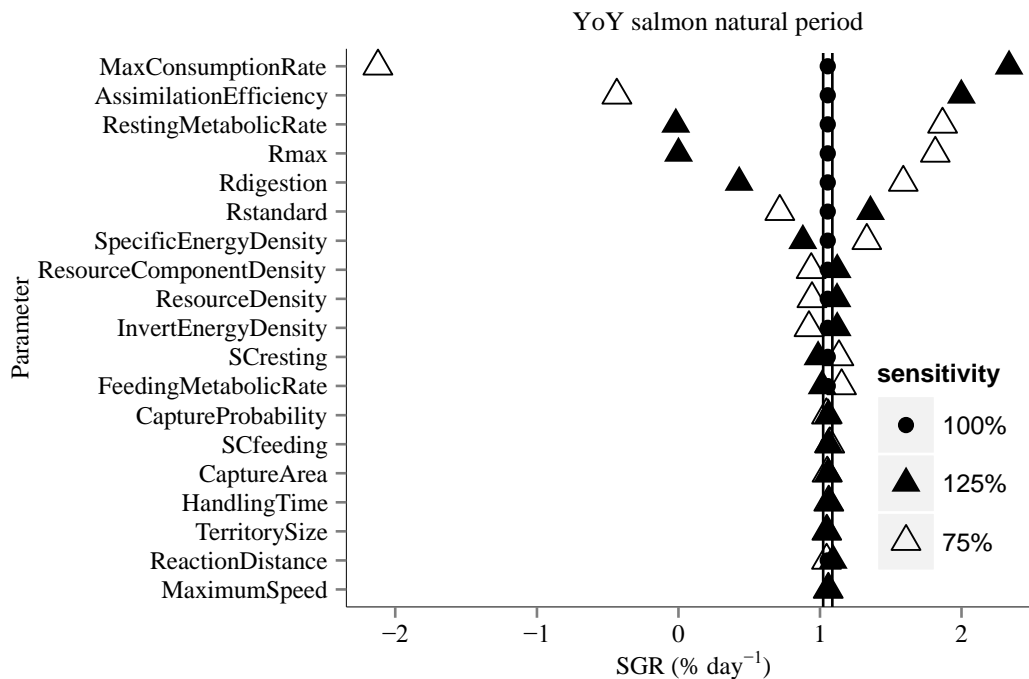


Figure 3.7. A sensitive analysis of parameters and how they affect the specific growth rates (SGR, % bodymass.day<sup>-1</sup>) of young-of-year (YoY) Atlantic salmon (*Salmo salar*) in the salmonid individual-based model (IBM) with parameters set at 75%, 100% & 125% of the best estimates obtained published literature sources. Parameters are ranked on level of impact.

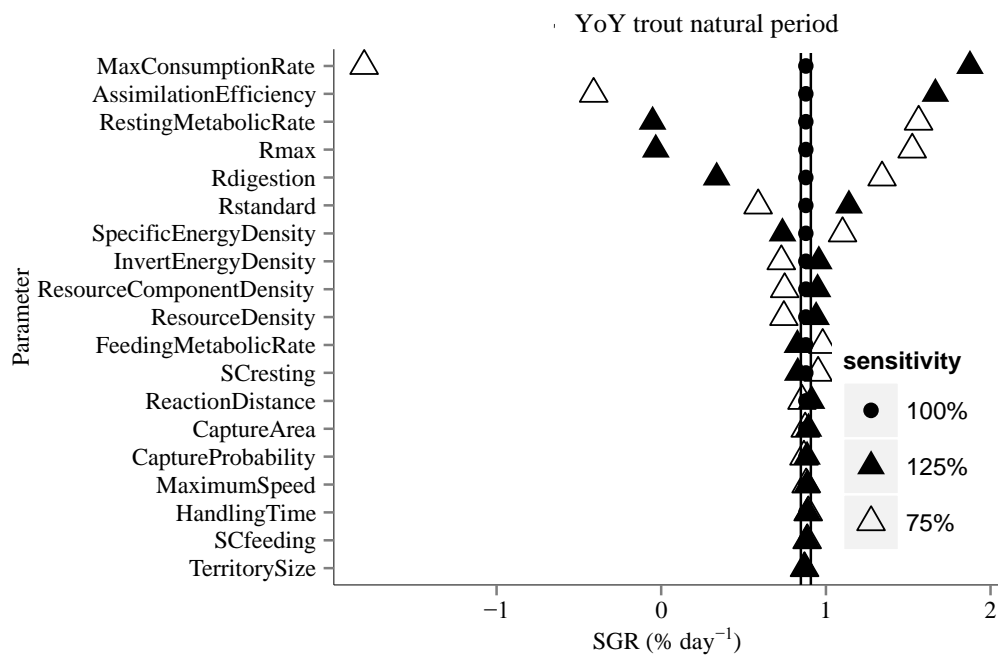


Figure 3.8 A sensitive analysis of parameters and how they affect the specific growth rates (SGR, % bodymass.day<sup>-1</sup>) of young-of-year (YoY) brown trout (*Salmo trutta*) in the salmonid individual-based model (IBM) with parameters set at 75%, 100% & 125% of the best estimates obtained from published literature sources. Parameters are ranked on level of impact.

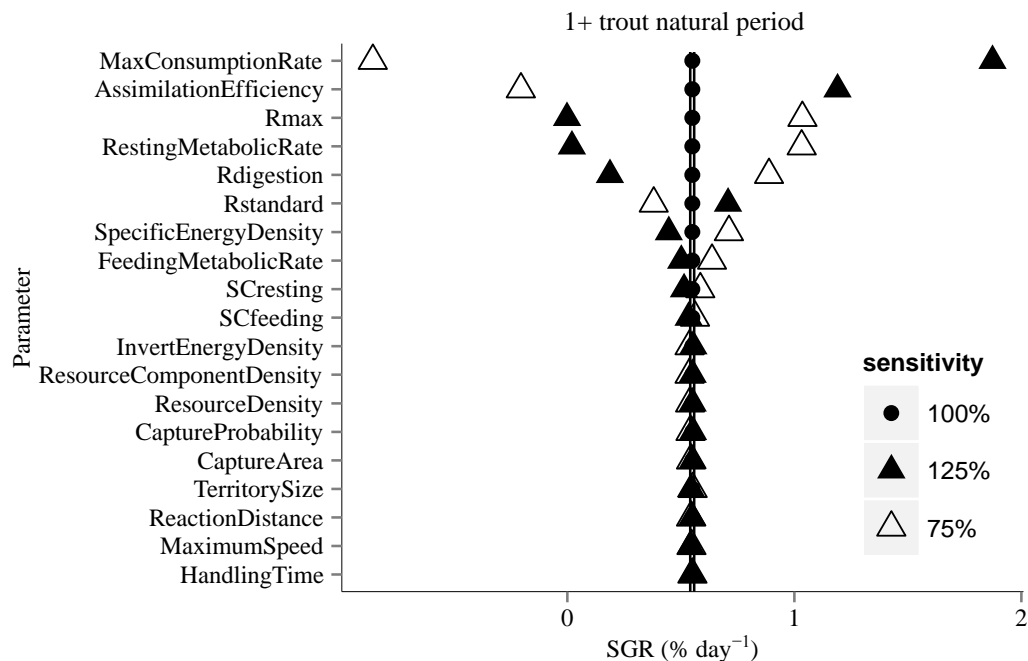


Figure 3.9 A sensitive analysis of parameters and how they affect the specific growth rates (SGR, % bodymass.day<sup>-1</sup>) of one-year-old (1+) brown trout (*Salmo trutta*) in the salmonid individual-based model (IBM) with parameters set at 75%, 100% & 125% of the best estimates obtained from published literature sources. Parameters are ranked on level of impact.

### *3.3.6 Impact parameter estimate on forager growth rates*

Variation in the parameter estimates caused a variation in predicted fish growth rates with the level of variation highest in the parameters of maximum consumption ( $C_{\max}$ , Figure 3.19) and digestive assimilation efficiency ( $R_{\max}$ , Figure 3.12) rates. Parameter estimates of assimilation efficiency (Figure 3.11) and standard respiration rates ( $R_{\text{standard}}$ , Figure 3.13) did not have as large of an impact on predicted forager SGR. Simulations using  $C_{\max}$  estimates drawn from its distribution resulted in the most varied spread in forager predicted SGR. Parameter estimates from the lower tail in their distribution resulted in negative growth rates in all three salmonids with the exception of for 1+ trout under conditions of low flow. The impact using parameter estimates drawn from a distribution on predicted salmonid growth rates depended on which flow period; predicted growth rates have a larger distribution than the SGRs under a regime of normal flow when compared with the predicted distribution in a period of reduced flow. This effect was present across all forager types for all parameters investigated.

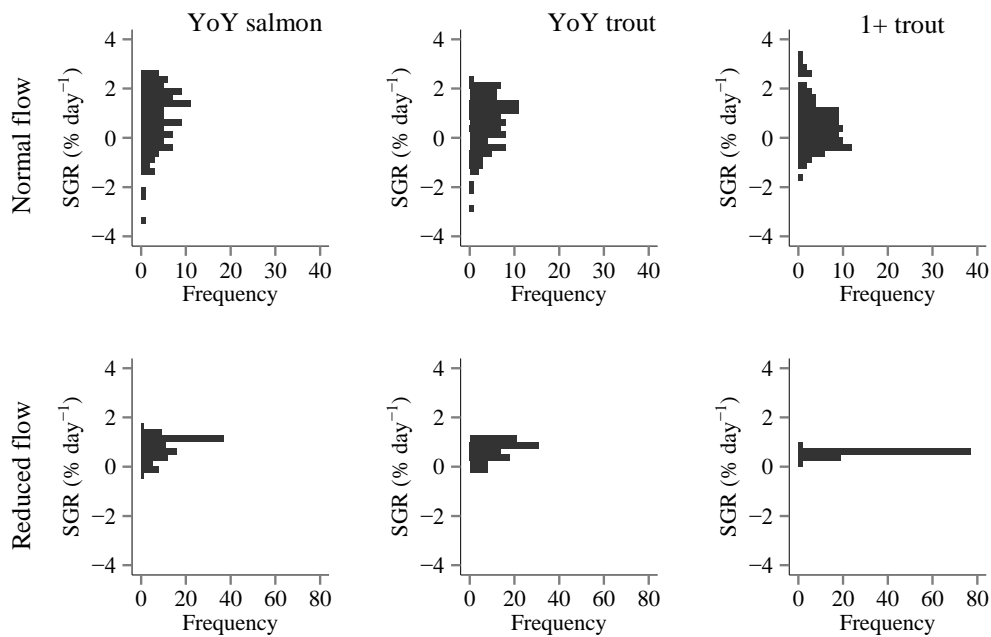


Figure 3.10 The distribution of mean specific growth rates of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) under two flow regimes predicted from a 100 simulations with the parameter of fish maximum consumption rate ( $C_{\max}$ ) drawn from a 95% confidence interval distribution adapted from Elliott (1976). All other parameters remained constant.

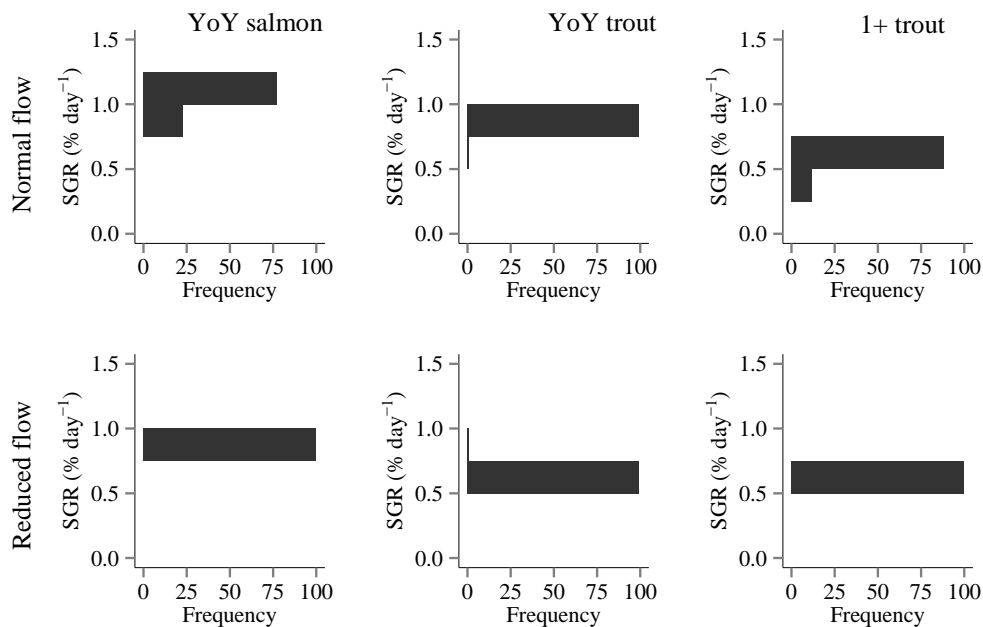


Figure 3.11 The distribution of mean specific growth rates of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) under two flow regimes predicted from 100 simulations with the parameter of fish assimilation efficiency drawn from a 95% confidence interval distribution adapted from Elliot (1976). All other parameters remained constant between simulations.

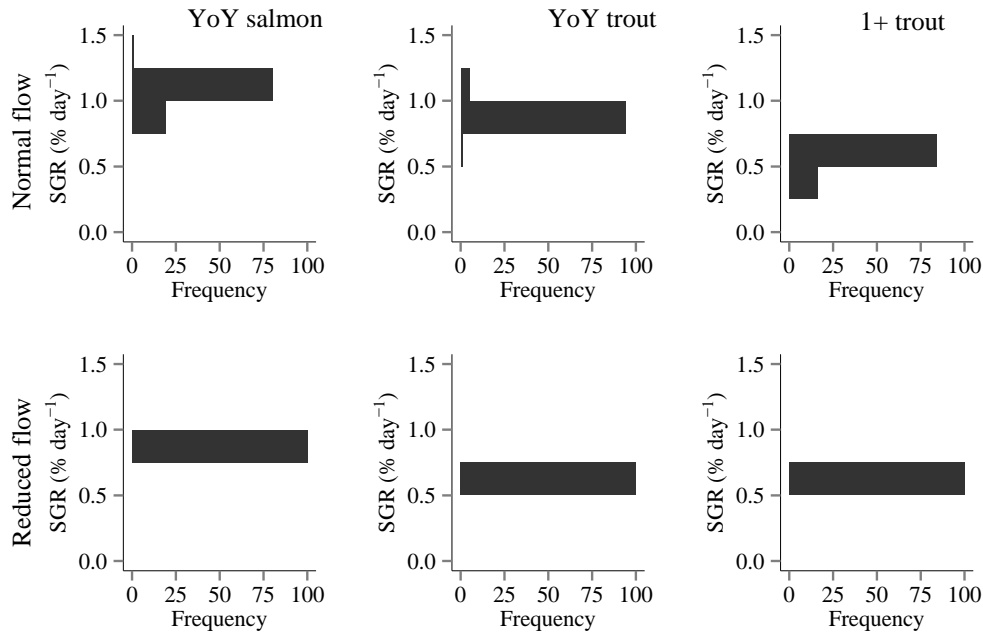


Figure 3.12 The distribution of mean specific growth rates of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) under two flow regimes from a 100 simulations with the parameter of fish maximum respiration ( $R_{\max}$ ) drawn from a 95% confidence interval distribution adapted from Elliot (1976). All other parameters remained constant between simulations.

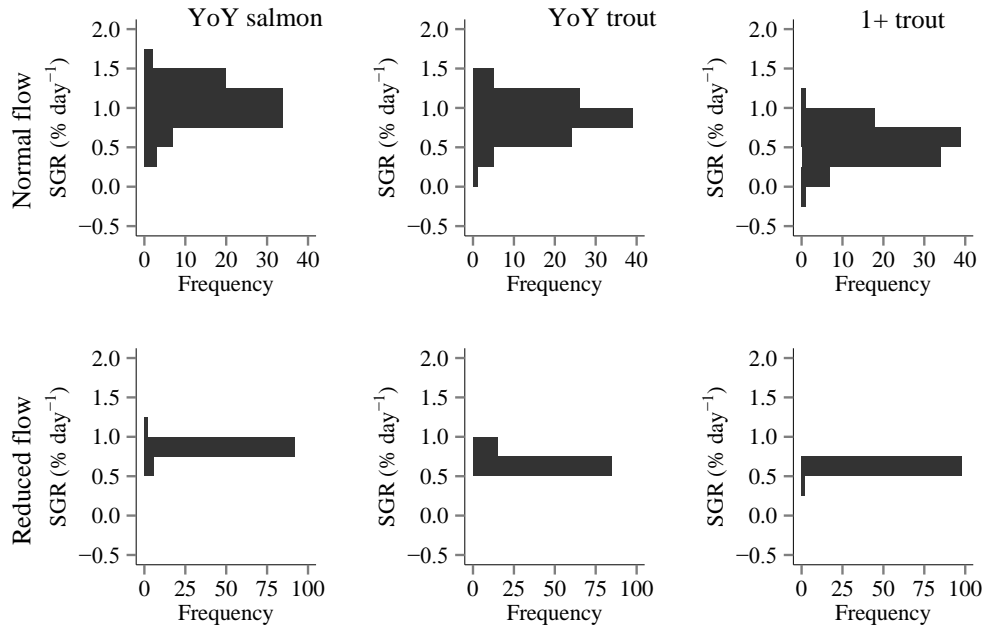


Figure 3.13 The distribution of mean specific growth rates of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) under two flow regimes predicted from a 100 simulations with the parameter of fish standard respiration rates ( $R_{\text{standard}}$ ) drawn from a 95% confidence interval distribution adapted from Elliot (1976). All other parameters remained constant between simulations.



### 3.4 Discussion

Population patterns of virtual salmonids in this individual based model closely resembled the population patterns of real fish under the same environmental conditions and this can be interpreted as a validation of model assumptions and internal structure. Virtual salmonids grew and distributed themselves in a similar fashion as real fish suggesting that the virtual individual behaves like a real salmonid. This is a successful example of an IBM approach used as a quantitative ecologically predictive model of freshwater fish and growth. The use of complimentary fieldwork data specifically collected to be used in statistical analysis between observed and predicted patterns is an approach that goes beyond the traditional standard of IBM validation in pattern-orientated modelling (see Grimm & Railsback 2005). It also shows the ability of the MORPH modelling platform to model fish populations.

IBMs are fundamentally different from traditional ecological models (Grimm & Railsback 2005). Though the underlying philosophy (the interactions occurring at the individual level determines the patterns seen at the population level) has long been established, the ability to model the numerous interactions was historically difficult but IBMs are increasingly accessible due to advances to computing power. Virtual individuals in this model are parameterised to be subject to the same bioenergetics (e.g. consumption and respiration processes), physiological properties (e.g. bodymass, drift feeding etc.) and behaviours (e.g. territory and size dominance) as salmonid fish (Elliott 1975; Elliott 1976; Hayes et al. 2000; Grant & Kramer 1990; Piccolo et al. 2008; Wankowski 1979). The similarity between population patterns of virtual and real fish validates the assumptions of how these parameters interact together to determine salmonid growth and distribution. If these were wrong, it is unlikely that the multiple patterns investigated would so closely match between virtual and real fish (Grimm & Railsback 2005). This is an example of how IBMs can

link behavioural studies at the individual level with predictions at the population and if used for conservation purposes, IBMs can be the tool to link the two that Caro (2007) calls for.

Whilst the model predicted population patterns are generally representative of observed patterns, it is better able to predict some patterns in certain foragers than others. The mean predicted growth rates of YoY trout do not significantly differ from observed SGRs and is an indication of high model predictive power for this forager class but the same level of predictive power is not observed for the other forager classes. Although the mean predicted SGR for 0+ salmon and 1+ trout were significantly different from the observed, these predicted SGRs fall within the observed min and max range with the exception of 1+ trout during the period of reduced flow. The importance of 'weak' pattern can also help validate model predictions (Grimm and Railsback 2005) and with the exception of 1+ brown trout, the model predicts a decrease in SGR under a reduced flow condition and this same pattern was also observed in wild fish.

Discrepancy between predicted and observed growth rates in YoY Atlantic salmon might be explained by slight physiological and behavioural differences between Atlantic salmon and brown trout. Whilst very similar generally, there are differences in the microhabitat use in Atlantic salmon and brown trout (Klemesten et al. 2003; Heggenes et al. 1999) possibly caused by differences in metabolic swimming performance (Pederson et al. 2008). These differences were not modelled and are a potential area that may require future development. An alternative reason may explain the difference in the growth rates of virtual and real 1+ trout and that is the limited number of behavioural options within the model with foragers only moving or feeding. This omits certain potentially bioenergetically expensive behaviours such as establishing and maintaining a territory (Grant & Kramer 1990; Johnsson et al. 1999). Brown trout exhibit territorial behaviour and as territory size is positively correlated with forager size,

larger individuals expend more energy in maintaining their larger territory (Bachman 1984). The inclusion of such a cost may lower predicted growth rates in 1+ trout and bring them more in line with observed rates. However, an interactive territorial behaviour would be highly complex to model and a simpler approach by a probabilistic cost associated with territorial behaviour may lead to similar results.

Virtual foragers distribute themselves in a similar fashion to observed foragers at both the scale of a stretch and that of a patch. Whilst statistical tests show some significant difference from perfect prediction in the distribution of trout, the importance in considering biases in the observed patterns must be considered; are the observations collected from fieldwork a 'correct' representation of what foragers are doing in the system? (see Johnson & Omland 2004; Quinn & Dunham 1983) The model always underestimates the population of 1+ trout in stretch 1, and whilst this may be interpreted as a poor predictive power of the model, the location of the stretch is at the end of the open system that is the field site and some of the observed population density may be from immigrating individuals from a higher density fish sections further downstream of section 1 (see Fig. 2.3, p32) and thus skewing the density. The accuracy of observations may also be biased when referring to difficulties in catching all fish in deep and/or fast flowing patches (i.e. stretch 5 and stretch 6 respectively; see chapter 2); but these observational biases will be prevalent in any ecological study. This line of reasoning is one argument against using statistical tests when validating IBMs, and is encapsulated in the 'pattern-orientated modelling' approach encouraged by Grimm & Railsback (2005). We have shown the ability of the model to predict observed patterns by that standard and the authors feel that the statistical approach is still a valid one as it provides an additional level of validation and will raise issues (e.g. open vs. closed systems) that can improve modelling and statistical methodology for future IBMs.

To increase comparative accuracy between predicted and observed results, it is possible to perform a ‘calibration’ step of an estimated parameter and have it configured to best match one set of patterns (Grimm & Railsback 2005). A good parameter candidate for this model would be the velocity a forager would swim at resting. Such a step would reduce the number of observed patterns remaining to validate model predictions at a later step. However, being better able to predict a specific set of observed patterns does not improve the potency of the model, as it would be configured for one scenario and thus lose overall applicability when applied to other systems or conditions. Considering this, model calibration was omitted and the model is still able to predict fish growth rates and their distributions under two distinct flow regimes.

For model simplicity, the model purposefully excludes some known factors that impact salmonids. One example is the impact the turbidity of the water has on the successful capture of a drifting invertebrate; the probability of a fish successfully capturing a prey item decreases as turbidity increases (Barrett et al. 1992). However, Harvey & Railsback (2009) found that salmonid feeding was negligibly affected at rates below 5 Nephelometric Turbidity Units (NTU) and as primarily ground water fed and low sediment loads, chalk streams are typically clear systems (Berrie 1992) and this effect was purposefully left out. If this model was to be applied to other river systems, depending on the river characteristics, the effect of turbidity may need to be included.

Model predicted variation in mean forager SGRs is always less than the variation observed from wild foragers (Figure 3.2 p91). The variation in observed SGRs may be caused by two reasons, 1) habitat heterogeneity and 2) individual trait differences leading to residual sampling error (SE) in mean SGR of the sample PIT tagged individuals. Within the model, there is little variation between foragers of the same forager type, only differing with their starting location and biomass.

As an optimal-foraging discrete individual model, MORPH is able to predict the effects of density dependence on population characteristics (Toral et al. 2012). In this instance of the salmonid-model, density-dependence processes that may cause population variation may not be expressed as the highly productive characteristics of chalk stream environments may mean that even comparatively poor patches will still meet the requirements for growth.

The majority of forager energetics is taken from the work done by Elliott (1975, 1976a, 1976b) into brown trout energetics. Their studies produced a mean estimate but there were observed variation and it is difficult to ascertain if this is derived from variation from very different individuals (different ages and sex; the bioenergetics of gamete production of a sexually mature individual are vastly different from a juvenile) or from similar individuals. Despite this, intra-specific variation between conspecifics had been observed and the investigation into parameter estimates on forager SGR show that variation in bioenergetics is a possible source of observed variation in population patterns. Investigating the effects of bias in parameter estimation also provided an alternative approach to understanding model predictions. By creating estimated parameters from a distribution and analysing the parameters independently it is possible to create a more robust understanding of predicted SGRs. This allows the creation of frequency distributions that display a range of predictions, from which probabilistic or likelihood functions of impacts (e.g. of alternative management regimes) can be derived, assisting interpretation of results. The increased realism in predicted SGRs (i.e. increased range of forager SGRs) indicates that the approach has much promise and should be investigated further in the future; a possibility is to incorporate more power statistical tests like Markov Chain Monte Carlo (MCMC) and Approximate Bayesian Computation (ABC) statistics during model construction and validation (Hastings 1970; Beaumont et al. 2002; Kass & Raftery 1995).

With a validated salmonid-specific IBM, the ability to manipulate parameters of environmental, population and individual traits afforded by an IBM approach will mean that future model variations can be used to investigate the impacts or changes at these scales. From a conservation perspective, the model could be used to investigate the extent to which chalk stream environments can tolerate climate change effects and other possible critical ecosystem stressors (Dudgeon et al. 2006). The highest recorded water temperature of chalk stream from the field data collected in this study was 19.6°C and this is near the temperature extreme of current bioenergetic understanding of brown trout bioenergetics (Elliott 1976). Brown trout stop growing at these temperatures (Elliott 1976) and thus, in light of predictions of climate change impacts on temperatures in the UK increasing by a mean of 4.2°C (Murphy et al. 2009), chalk stream management must start proactive measures to safeguard their salmonid populations. IBMs can provide environmental managers with a ‘virtual laboratory’ and should be an utilised tool to predict how the system will respond to the change and just as importantly, how it will respond to the different proposed management regimes (Zurell et al. 2010).

As with all models, the potential to include extra parameters and interactions will always remain but it should be done with caution, as it needs to be ascertained if inclusion of more parameters and complexity is a worthwhile process (Grimm & Railsback 2005). Sensitivity analysis of input parameters identifies the ones that are most suitable for simplification but these could be useful in future investigations especially if the impacts on individual physiological traits are investigated (e.g. impacts of parasites on feeding success – Barber et al. 2000).

A validated salmonid IBM is a powerful predictive model that should be added to the current chalk stream management model toolbox to inform management decisions. Its different approach to modelling ecology

(‘bottom-up’) will be a compliment to current models and should be viewed complimentary and not as a rival (Grimm & Railsback 2005). The ability to apply site-specific environmental data to a generic salmonid-specific IBM to tailor management regimes specifically for each site is just one potential it provides. Whilst still in a relatively early stage of development, the current ability of this IBM to predict observed patterns is evidence of its predictive power and lending to the promise of IBMs to help move from reactive to proactive fishery management.

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## **4. Accounting for density dependence and prioritising salmonid conservation management**

### **4.1 Introduction**

Chalk stream salmonid fisheries in southern England are a lucrative industry and are an important natural resource for local communities (Mawle & Peirson 2009). Resident populations of brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) are two species targetted by anglers in these chalk stream fisheries. Unfortunately, a global decline in Atlantic salmon numbers has been observed (Parrish et al. 1998) and wild Atlantic salmon stocks in the UK are not immune to this decline, reflected in lowered adult salmon catch across the country (Environment Agency 2004). The UK has extensive management schemes for Atlantic salmon conservation at both the local and national scales but success has been mixed; whilst the total number of rivers containing spawning populations of Atlantic salmon has increased, overall population numbers are down (Environment Agency 2004). Given the high economic and ecological value of Atlantic salmon stocks, there is a need for a constructive evaluation of current freshwater management regimes in addressing the decline in their numbers (Bisson et al. 2009). Furthermore, this understanding needs to include the impacts management regimes associated with Atlantic salmon conservation have on the other salmonid populations (e.g. brown trout) in mixed chalk stream fisheries.

Fishery management regimes can aim to increase fish densities either by population enhancement or by improving habitat quality (Rosenberg et al. 2000; Nagata et al. 2012). In salmonid management, population enhancement regimes attempt to directly increase population numbers by measures such as stocking (the addition of fish, typically farm-reared) or improving natural recruitment (e.g. gravel cleaning to improve egg and larval survival rates). Alternatively, other regimes (e.g. encouraging in-stream and bankside vegetation growth) target habitat quality by removing

limitations in the environmental conditions, to allow for a higher carrying capacity (Armstrong et al. 2003). These commonly adopted management regimes are theoretically sound but the practical success of each approach in achieving management goals may be inhibited by site-specific characteristics that may limit their effectiveness (Bisson et al. 2009; Burnett et al. 2007).

Management regimes that incorporate site-specific abiotic and biotic parameters during their design will have a higher chance of success than regimes that do not (Saunders et al. 2002). This need is especially true in freshwater habitats where sites along a river can exhibit highly heterogeneous characteristics (e.g. in-stream vegetation, sediment, riparian vegetation, water abstraction, etc.) within a relatively short distance. Atlantic salmon and brown trout have distinct habitat requirements (Armstrong et al. 2003) thus placing a premium on the habitat characteristics of a site when designing management regimes. An example of mismanagement of resources would be the futility of stocking salmonids at a site lacking the required habitat requirements. Conservation scientists need to provide managers with tools that help inform decisions by evaluating the effectiveness and efficiency of alternative regimes and approaches.

In this chapter, we use a previously described and validated salmonid individual-based model (see chapter 3) to perform scenario testing to predict the impacts of 1) stocking of young-of-year Atlantic salmon; 2) changes to food resource density associated with habitat restoration; 3) changes to habitat size associated with habitat construction on the growth rates and distribution of Atlantic salmon and brown trout. Model predictions are used to evaluate regimes on their effect on smolt survival in a context of Atlantic salmon conservation.

## 4.2 Methodology

### *4.2.1 Virtual environment*

The virtual environment used in this investigation is based on the Mill Stream environment 2008 dataset (see chapter 2). Any changes to the dataset and model are outlined here.

### *Scenario testing*

The effect of three management regimes on salmonid growth rates were investigated:

1. Increasing YoY Atlantic salmon population size (i.e. mimicking a management regime of stocking or gravel cleaning),
2. Improving habitat quality with an effect of increasing invertebrate drift densities
3. Increasing habitat area (i.e. a regime of restoring previously unsuitable chalk stream habitat).

The baseline scenario was observed conditions in the Mill Stream in 2008 and each scenario was tested from 50% to 150% of those conditions in 10% increments with management regimes simulated independently.

#### *4.2.2.1 Increasing YoY Atlantic salmon densities*

This scenario tests the effect increasing densities of YoY Atlantic salmon has on the chalk stream salmonid population. Baseline population densities are representative of the observed YoY and 1+ salmonid population structure in the Mill Stream in 2008 (see chapter 2). Simulations were run with modified population densities of YoY Atlantic salmon with brown trout densities kept constant at baseline densities. All other forager and environment parameters kept the same (see chapter 2 and 3). The starting number of YoY Atlantic salmon was rounded up to the nearest whole integer (i.e. whole fish) with scenarios from 50% to 150% of baseline population in 10% increments.



#### *4.2.2.2 Habitat quality – resource densities*

A regime of improved habitat quality was modelled by changing the resource drift densities from 50% to 150% of baseline densities in 10% increments (see chapter 2 for an overview of baseline densities of invertebrate drift). The properties of the invertebrate drift (i.e. size distribution, inter-stretch density differences and temporal variation) remained the same as in the baseline.

#### *4.2.2.3 Habitat area – patch size*

The effects a management regime of increasing habitat area was modelled by increasing the size of each patch in the virtual model. Patch sizes ranged from 50% to 150% of baseline size in 10% increments. Patch characteristics of mean depth, flow (i.e. run vs. slack flow) and mean velocity were kept constant at baseline (see chapter 2).

### *4.2.3 Modelling details*

#### *Simulation period*

The length of time during a model simulation was the period of natural flow (see chapter 2). The virtual environment is kept as the conditions in the natural flow period with any changes outlined in the description for each specific scenario.

#### *Model replicates*

Simulations of the same parameter set were replicated 5 times to capture model variability (see chapter 3).

#### *Baseline mean bodymass*

The effect of the scenarios on the size distribution of salmonid populations was investigated by counting the number of ‘large’ individuals of YoY Atlantic salmon and brown trout at the end of each simulation. A fish was

considered to be ‘large’ if its final bodymass was greater than the threshold defined as the mean bodymass for its specific forager class as predicted under a baseline scenario (i.e. natural conditions and no management). Increased bodymass is associated with increased overwinter and smolt survival in salmonids (Murphy et al. 2006).

*Statistics – specific growth rates*

The growth rates of the population was measured as specific growth rates (SGR) in  $\Delta\%$  bodymass  $\text{day}^{-1}$  by the equation:

$$SGR = \frac{\ln(W_{salmonid\ t_n}) - \ln(W_{salmonid\ t_0})}{t_n - t_0} * 100$$

Where SGR is the specific growth rate; W is forager body mass;  $t_0$  is the start of simulation period and  $t_n$  is the end of simulation period.

## 4.3 Results

### *4.3.1 Forager specific growth rates*

Predicted mean specific growth rates (SGR) for YoY Atlantic salmon and YoY brown trout showed a negative relationship with increasing YoY Atlantic salmon population density (Figure 4.1). Predicted mean  $\pm$  S.E. SGR (% bodymass day<sup>-1</sup>) for salmon was highest at densities at half of observed population density (50% of baseline) at  $1.18\% \pm 0.004$  and was lowest at 150% of observed population density with  $0.83 \pm 0.005$ . YoY brown trout SGR showed the same max and min relationship with population densities as Atlantic salmon, with  $0.98 \pm 0.005$  and  $0.69 \pm 0.013$  (mean  $\pm$  S.E. growth % bodymass day<sup>-1</sup>) for 50% and 150% YoY Atlantic salmon population densities respectively. Increased YoY Atlantic salmon density also lead to increased variation in predicted SGR caused by a decreasing minimum SGR observed. Maximum SGR remained fairly constant (mean  $\pm$  S.E.)  $1.64\% \pm 0.014$  and  $1.27\% \pm 0.01$  for salmon and trout populations respectively, for all simulated salmon population densities.

The opposite trend was predicted for the scenarios of increased habitat quality (i.e. increased resource density) and increased habitat area. In these scenarios, the predicted SGR was lowest in the 50% of baseline environmental conditions scenario and highest at the other end of the spectrum (150% of baseline).

The growth rates of 1+ trout showed very little variation in response to changing environmental conditions under the different scenarios of management regimes.

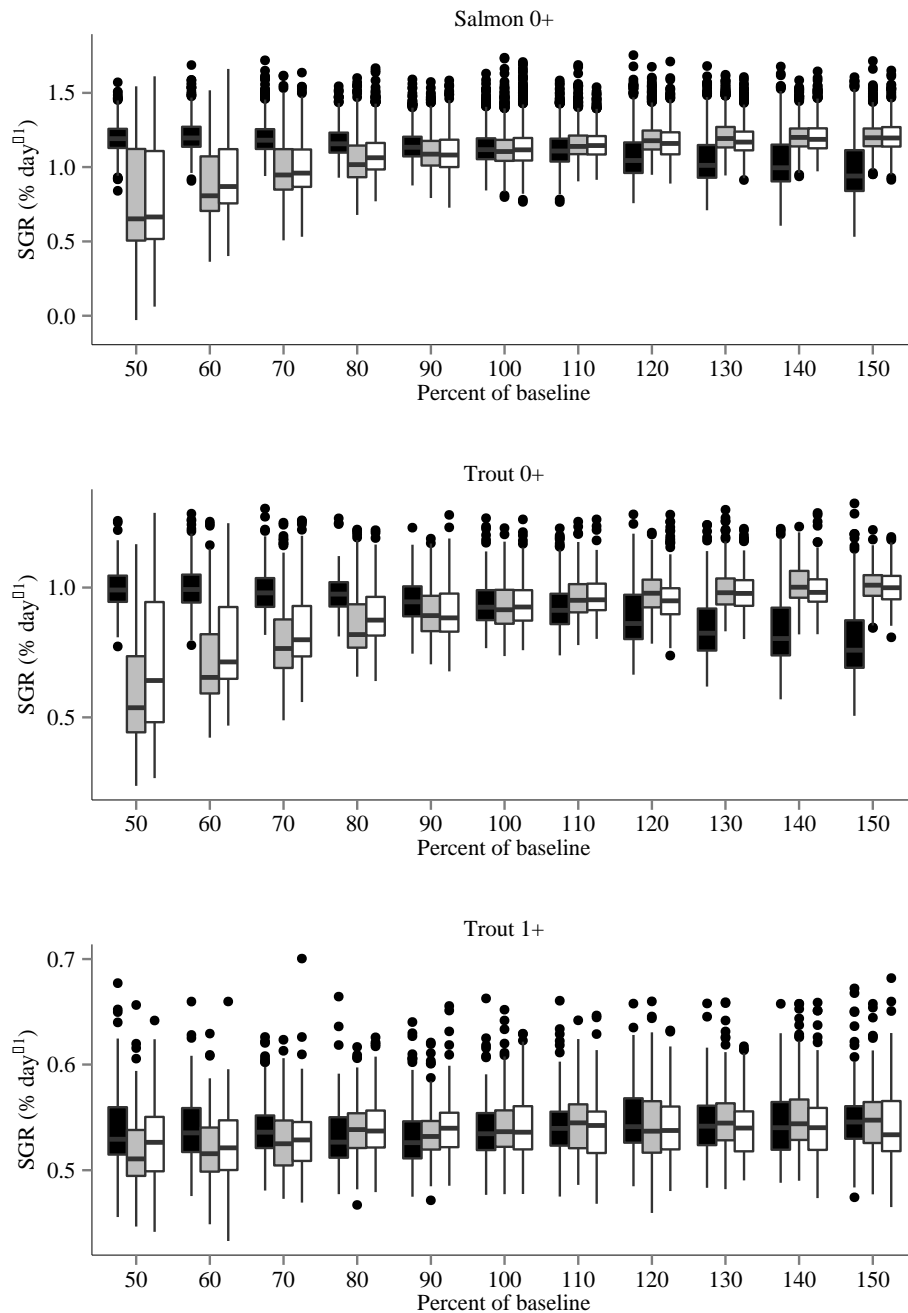


Figure 4.1 Predicted forager growth rates under scenarios of management regime induced impacts on the chalk stream habitat; manipulation of the population density of young-of- year Atlantic salmon (*Salmo salar*) (black ■); altering of the amount of food available/resource density (grey ■) and the amount of habitat available/patch size (white □). Boxplots show the median (dark line), inter-quartile range (box) and 1.5 standard deviation range (whiskers) and outliers (dark dots).

#### *4.3.2 The number of 'large' individuals*

Predicted mean YoY Atlantic salmon, YoY and 1+ brown trout body mass under 'baseline' environmental conditions (i.e. natural conditions as observed during fieldwork) was calculated to be 9.1, 15.0 and 98.4 g respectively. For each scenario, foragers predicted to have a final bodymass above their 'natural' group mean bodymass (baseline conditions) were defined as 'large' (Figure 4.2). The mean number of 'large' YoY Atlantic salmon showed a positive relationship with increases in resource density and habitat size. Under conditions of 50% resource density, the number of 'large' individuals was half that predicted at baseline. This same result was produced at 50% patch size. Under scenarios of 150% resource densities and patch size (independently) there was a positive increase in the number of large individuals. This same relationship is observed with increased YoY Atlantic salmon densities but the number of large individuals begins to plateau with YoY Atlantic salmon densities 20% above baseline.

This same positive relationship between increased patch size and prey resource density with number of foragers with bodymass above mean baseline bodymass is observed with YoY trout. There is however, a negative relationship between 'large' YoY brown trout and Atlantic salmon densities above 100% of baseline. The number of 'large' YoY trout is not affected at salmon densities below baseline. The number of 'large' 1+ trout does not show a relationship with changes to environmental parameters tested. The number of 'large' 1+ trout varied from 9 to 11 individuals across all scenarios.

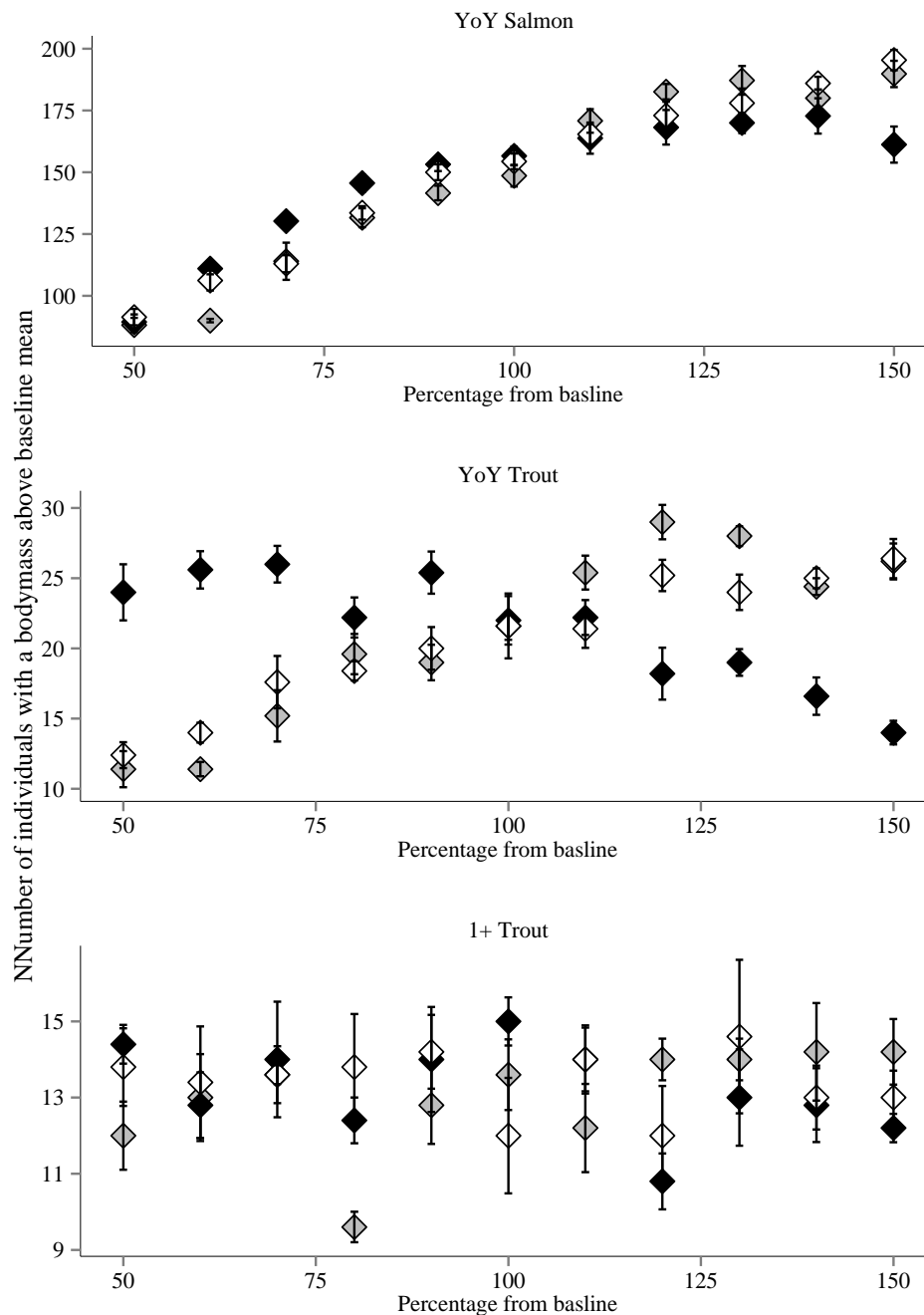


Figure 4.2 The predicted number of 'large' fish at the end of the simulated period under varying environmental conditions associated with management regimes; young-of-year (YoY) Atlantic salmon (*Salmo salar*) density (black ■), resource (food) density (grey ■) and habitat/patch size (white □). The diamond represents the mean with error bars indicating the S.E. from 5 model replicate simulations. The three forager classes are YoY Atlantic salmon (top graph), YoY brown trout (*Salmo trutta*) (middle graph) and one-year-old (1+) brown trout (bottom graph). A 'large' fish is a fish that has bodymass greater than mean bodymass under baseline (observed) conditions at the end of the modelled period.

#### 4.3.3 Population structure of YoY Atlantic salmon

The percentage of ‘large’ YoY Atlantic salmon increased from less than 30% to more than 50% of the total YoY Atlantic salmon population under scenarios of increased resource density and patch size. Contrastingly, at YoY Atlantic salmon population densities below 100% of baseline, ‘large’ YoY Atlantic salmon constitute on average around 50% of the entire population, but this falls to about 30% when total population densities increases to 150% of the baseline (Figure 4.3).

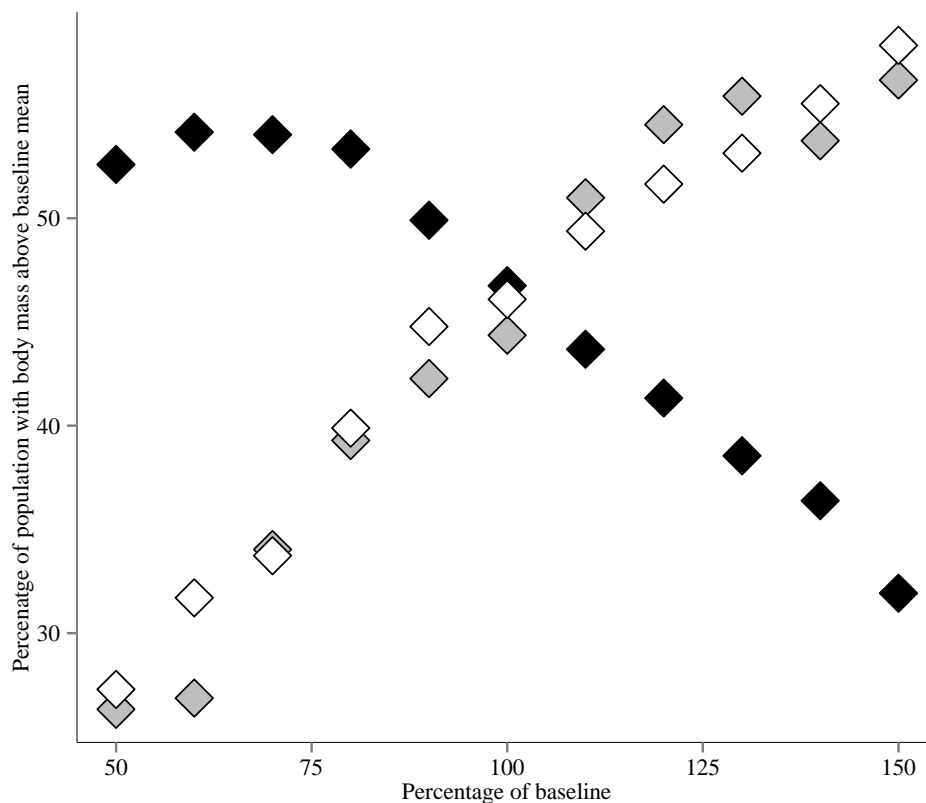


Figure 4.3 The mean proportion of ‘large’ young-of-year (YoY) Atlantic salmon (*Salmo salar*) as a percentage of the total YoY Atlantic salmon population under various environmental conditions associated with management regimes; YoY Atlantic salmon densities (black■), resource (food) densities (grey■) and habitat/patch sizes (white□). A ‘large’ fish is a fish predicted to have a bodymass (g) greater than the predicted mean population bodymass under baseline (observed) conditions at the end of the modelled period.

#### *4.3.4 The bodymass distribution of YoY Atlantic salmon*

A decline in mean population bodymass of YoY A. salmon is predicted under scenarios of increased population densities. Mean YoY Atlantic salmon bodymass is highest at population density 50% of the baseline with an estimated mean of  $9.58\text{g} \pm 0.08$  but this falls to  $8.40\text{g} \pm 0.05$  (mean  $\pm$  S.E.) as population density increased to 150% of baseline densities. The distribution of final body mass shows a greater variance with increased population densities (Figure 4.4). The minimum predicted forager bodymass decreases as population density increases with a minimum predicted YoY Atlantic salmon weight of 4.6g and 3.6g under 50% and 150% of the baseline population densities respectively. Maximum bodymass remained fairly constant across all simulated population densities at is  $17.9\text{g} \pm 0.18$  (mean  $\pm$  S.E.).



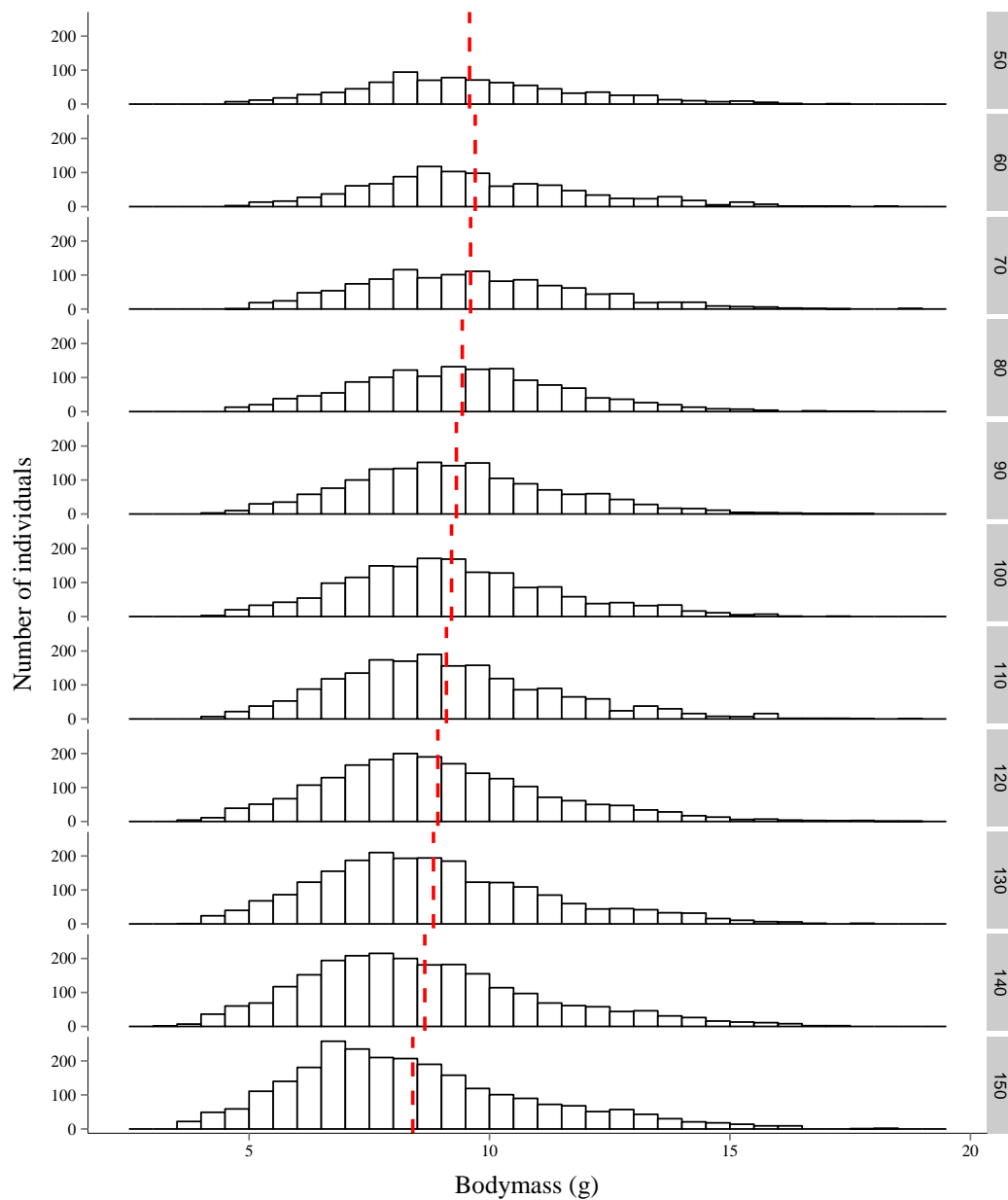


Figure 4.4 The predicted effect of population density on the population distribution of body mass of young-of-year (YoY) Atlantic salmon (*Salmo salar*) with no change to other environmental conditions. Population densities (grey box) are relative to the observed natural population density (100%). The dashed line shows the mean population body masses for each respective distribution.

#### 4.3.5 Proportion of feeding behaviour in a timestep

In response to the simulated parameter changes, foragers spent varying amounts of time feeding (Figure 4.5). YoY Atlantic salmon spent most time (10.7%) feeding under conditions of low resource density (50% of baseline) but this declined to 6.9% at 150% resource density. A similar negative relationship of a decrease in time spent feeding predicted for increasing YoY Atlantic salmon population density. This is contrasted by a positive relationship between time spent feeding and increasing patch size with time spent feeding 6.8% increasing to 8.6% at patch size of 50% and 150% of baseline respectively.

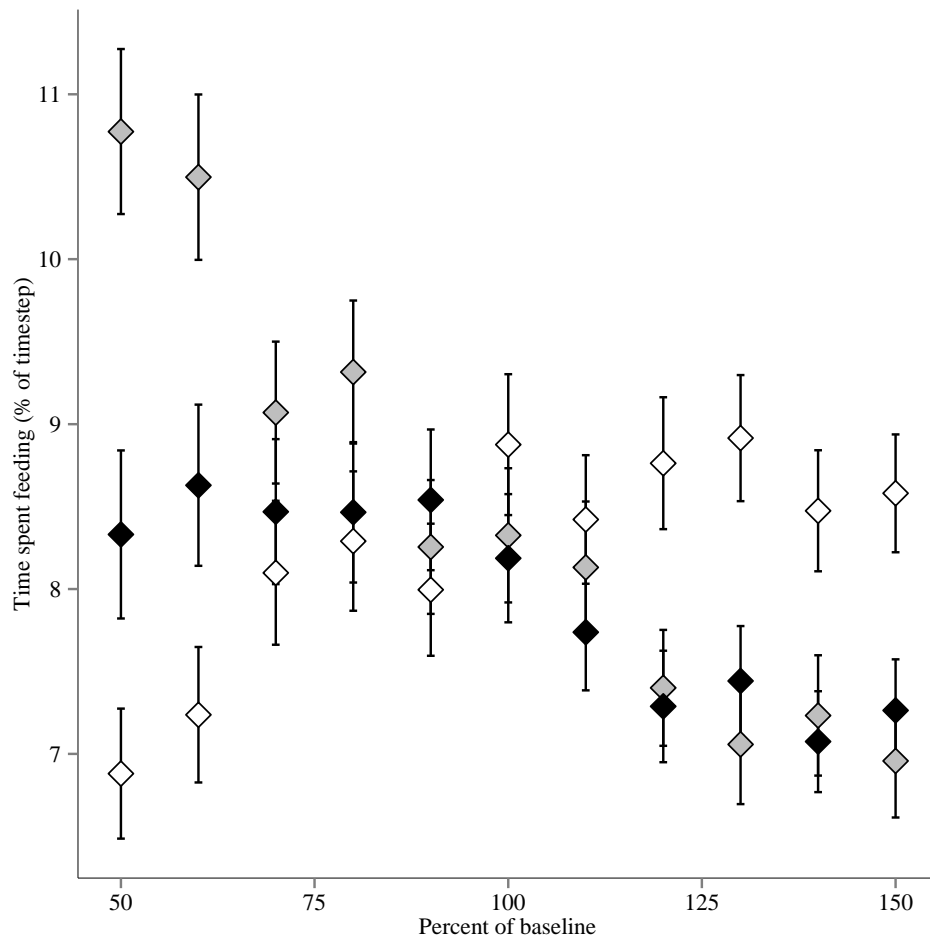


Figure 4.5 The mean time spent feeding by young-of-the-year (YoY) Atlantic salmon (*Salmo salar*) population at the final timestep of the model under various environmental conditions associated with common management regimes; total YoY Atlantic salmon densities (black ■), food availability/resource density (grey ■) and habitat (patch) size (white □).

## 4.4 Discussion

Predicted variation in the effect of management regimes indicate there is a need for management to identify the process pathway of regimes prior to implementation, as it will determine regime efficacy. A positive relationship is predicted to occur between all simulated management practices and YoY Atlantic salmon growth with the total number of 'large' fish increasing, however, this reached a plateau with the population enhancement regime as above a threshold YoY Atlantic salmon population density the number of 'large' fish did not increase and a negative effect on mean population growth rates in both YoY Atlantic salmon and brown trout is predicted. Whilst no effect was predicted to occur in larger 1+ trout, the effect on YoY salmonids growth rates needs to be interpreted with respect to population impacts so that the correct management regime can be implemented.

The distribution of forager specific growth rates in YoY Atlantic salmon populations is predicted to increase in variation and this is most likely due to density dependent processes. Specific growth rates are biologically maximally limited (Elliot 1976a) and the observed greater variation in forager growth rates is driven at the lower-tail end with more, and slower, growing fish (Figure 4.4). Salmonids exhibit strong territorial behaviour and there is competition for space to feed (Grant et al. 1998). As chalk streams are highly productive (Edwards & Owens 1960), it is likely that the underlying cause for fish growth is not related to the lack of food but rather the use of sub-optimal patches and/or limited feeding areas. Salmonids feed on invertebrate drift by taking a stationery position within the water column by swimming at the same speed as the water flow (Hayes et al. 2000), and with growth a function of both energy consumption and expenditure (Elliott 1976a), the occupancy of patches with higher velocities will present a higher energetic tax on the fish resulting in lowered growth. These sub-optimal patches may have low food densities (i.e. fish have to spend more time feeding to reach satiation, Figure 4.4) or higher velocities (i.e. fish have to expend more energy to feed). If the energetic costs associated with

feeding behaviour within a patch exceeds the energetic costs associated with not-feeding (or resting), it is bioenergetically advantageous to minimise energy loss by altering time budgets and feeding less. This behaviour constitutes a ‘non-aggressive energy-minimising’ strategy (Puckkett & Dill 1985; Titus 1990).

As a result of the territorial behaviour of salmonids, the area a fish can successfully feed may be a limiting factor in scenarios of high population densities and this may also explain predicted lower salmonid growth rates (Keenleyside & Yamamoto 1963; Grant & Kramer 1990). As the number of fish increases, the competition for the resource of feeding space increases up to the point that some fish cannot establish territories and hence are unable to feed. The relationship between space, territory size and salmonid population density has been used to estimate the carrying capacity of a site (Ayllon et al. 2012; Grant & Kramer 1990; Grant et al. 1998). A salmonid IBM approach is another potential tool that can also estimate a site’s carrying capacity and should prove a valuable management tool. Identifying that the population density at a site is already at carrying capacity will allow management decisions to select another site for population enhancement or adopt management regimes that aim to improve the habitat so a higher population density can be supported.

There are a number of negative effects associated with increasing population densities that should factor into management decisions. Firstly, increasing numbers of YoY Atlantic salmon parr (increased population density above a threshold produces more small fish – Figure 4.4) may not contribute to the overall management aim of more adult fish. Atlantic salmon parr may spend 1 – 6 years in freshwater habitats and have to survive at least one winter season before smolting and migrating seawards (Okland et al. 1993). The winter period of chalk streams are marked by reduced productivity and higher flows and pose a significant challenge to salmonids (Murphy et al. 2006). As salmonid overwintering survival rates is

positively related to fish size (Ebersole et al. 2006), mortality in smaller YoY Atlantic salmon will be high and these individuals are less likely to survive to grow into adults. Secondly, changing the population structure can also impact on population stability. The trigger for Atlantic salmon to smolt is likely to be the attainment of a critical body size, and of the smaller growing fish that do survive the winter, smolting may be delayed to remain in freshwater to grow more before smolting in a subsequent season (McCormick et al. 1998). A higher retention of Atlantic salmon parr will alter the population structure that might lead to greater competitive interactions between 1+ and YoY Atlantic salmon parr and potential delayed implications need to be considered by management.

Increasing the density of Atlantic salmon will increase both intra and interspecific competition in the system. Thus population enhancement regimes that raise population densities above the carrying capacity of a stretch of river might actually result in lowered overall population cohort fitness. In addition to impacts on growth rates and survival, further negative impacts may come from increase incidences of disease and/or greater attraction from predators (Jepson et al. 2000). This translates to a scenario where stocking of Atlantic salmon may ultimately impact the number of adult fish returning (Aprahamiam et al. 2003). Interspecific competition can also lead to negative impacts on other salmonid populations; YoY brown trout growth rates declined as YoY Atlantic salmon numbers increased (Figure 4.1) which is a potential conflict in mixed fisheries. Additionally, the alternative is also true in that if a fishery stocks brown trout, Atlantic salmon growth rates are likely to be impacted. Given the size dominance structure of salmonid behaviour (Deverill et al. 1999), impacts are likely to be greater on YoY salmonids if stocking of older, larger conspecifics. However this is less clear given an observed lower competitive ability of farm-reared salmonids when compared with wild conspecifics (Deverill et al. 1999). Furthermore, stocking with reared fish is a threat to stock genetics (Aprahamiam et al. 2003) and so a stocking regime for either fishing or for

conservation purposes needs to be evaluated for the future sustainability of salmonid stocks. Nonetheless, although similar salmonid species, brown trout and Atlantic salmon occupy similar but slightly different niches and it is unlikely that one species will completely outcompete the other (Heggenes et al. 1999).

If competition for limited optimal patches is an underlying cause of lowered growth rates and smaller fish, management should address the issue of sub-optimal habitats and limited space (Burnett et al. 2007). Rivers can be engineered and modified to increase optimal habitat (e.g. habitat restoration regimes, De Jong et al. 1997). However, caution must be exercised with such an approach; a patch is characterised by many variables and an ‘optimal’ status will only exist within a specific set of habitat and forager characteristics. Appreciation of environmental variation (e.g. drought or temperature fluctuations) can quickly disqualify optimal status and so there is a need for a varied, heterogeneous environment to ensure the existence of a population (Bisson et al. 2009).

Understanding the effect of management regimes on YoY salmonid populations is key to evaluating their efficiency and efficacy and is an important step to evidence-based management. Regimes can be designed to overcome some of the negative impacts of density dependent processes by understanding the characteristics of the drivers for these processes (Allyon et al. 2012). These interactions will differ between sites and evaluating and adopting a management regime that is tailored for the site provides the best pathway to achieving management aims. Finally, conservation scientists should assist by providing management with predictive tools and as shown here, IBMs are potentially powerful tools that can help address this.

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## **5. Assessing parasite risk by predicting population responses to the impacts of host-parasite relationships**

### *5.1 Introduction*

Parasites exert a significant influence on host population dynamics (Lafferty et al. 2008, Hudson & Greenman 1998) and the overall ecosystem (Poulin 1999). When introduced, non-native parasites can have an especially detrimental impact on host populations as the host may not have developed adequate defence response and thus the parasite will impact population health, alter disease emergence patterns in the ecosystem and overall community diversity (Okamura & Feist 2011, Peeler et al. 2011, Gozlan et al. 2006). The challenge for conservation management is to predict the magnitude the impact the introduction of a non-native parasite will have on a population prior to infection (Dunn et al. 2012); the risk of a reactive approach is that parasite-induced impacts on a population may only be observed at a stage when management intervention is too late to be effective (McCallum & Dobson 1995).

The typically small size of parasites belies their total impact as they impact all trophic levels and this results in a cumulatively large exertion on the total energy flow in an ecosystem (Kuris et al. 2008). Infection will result in sub-optimal host health and this warrants attention from environmental managers, especially if the host species has high economic and/or ecological value (Scott 1988). Parasite infections deplete host energy either directly (i.e. parasitic consumption of host energy stores or tissue) or indirectly (e.g. infection leading to a host immune response or affecting host movement cost) (Bakke & Harris 1998). It is difficult to study the total impact parasites have in natural systems as diseased and infected individuals are removed from possible observation either by predation or death, additionally, some nonlethal parasite impacts may only present on host fitness at a later period (Dybdahl & Lively 1998).

Individual-based models (IBMs) model the interactions between individuals within a population and their interactions with their environment. This approach has the potential of bridging knowledge from host-parasite studies (interactions at the individual levels) and how these impacts translate to the population. It can be used to study impacts of specific diseases (e.g. parapoxvirus in red squirrels, see Rushton et al. 2000), but there has been no attempt to investigate the impacts on populations by classifying and grouping by type of host-parasite interaction. An approach that investigates the type of parasite impact independently will provide a theoretical understanding of host population susceptibility to that impact route. The alternative, studying the impacts of a specific parasite, will result in studying the effects of multiple impacts as parasites affect hosts through several pathways (e.g. Barber et al. 2008). By separating impacts, it may be possible to identify the pathway a host population is most sensitive to and this will help prioritise management concerns.

In this chapter, a previously defined and validated salmonid-specific IBM is used to investigate the *in fine* parasite impacts on a salmonid population. The extent to which a parasite impacts its host fish is dependent on a multitude of factors, including but not limited to the species of parasite, the life-stage of the parasite, the host and associated condition factors as well as the biotic and abiotic properties system they exist within (Barber et al. 2008; Francova & Ondrackova 2013). This investigation will focus on three types of impacts experienced by parasitised fish involving alterations to the host i) bioenergetic budgets, ii) foraging/locomotive mechanics and iii) host behaviour. The aim is to identify the hierarchy of impacts that are most capable of impacting salmonid interactions by investigating the most common impact pathway associated with salmonid parasites. This provides a wider conceptual perspective that will have added benefit with poorly understood parasite species with the overall goal to help management strategise plans to deal with parasites.

## 5.2 Methodology

### *5.2.1 Salmonid IBM overview*

The salmonid IBM used in this investigation is the same as described in Chapter 3. Modifications that have been made to forager parameters are outlined here. Environmental parameters were not modified and remained constant for each model simulation.

### *5.2.2 Parasitised fish*

At the start of a model simulation, every forager has a 30% probability of being ‘parasitised’ based on observed levels of parasitism in fish populations (Britton et al. 2011). Foragers remain parasitised throughout the entire simulation and parasite transmission between foragers is not modelled so non-parasitised fish will remain parasite free for the entire simulation. The total number of foragers (parasitised + non-parasitised) remains consistent with the original model.

### *5.2.3 Parasite impacts*

A total of seven different scenarios of parasite-host interactions covering a total of five different parasite impacts (three physical and two behavioural) are investigated (Table 5.1).

Table 5.1 The description of host-parasite impacts, host responses and model modifications used to define seven separate scenarios to test parasitic effect on salmonid populations.

Scenario	Type of parasite impact	Parasitised host response	Modification to the model	Intensity of impact
1	Parasite consumption of host bioavailable energy	-	Reduction in assimilation efficiency	0 – 20% (5% increments)
2	Affliction of host food capture sensory system	-	Reduction in reaction distance	0 – 20% (5% increments)
3	Increased drag or reduced motor efficiency	-	Increased swimming costs	0 – 20% (5% increments)
4	Reduced competitive ability of host	Reduced ability to establish territories	Parasitised fish are processed after their non-parasitised conspecifics	Non-parasitised fish are processed first: parasitised fish are processed last.
5	Change in predation perception	Do not consider predator density when selecting patch	Parasitised fish have altered fitness measures of patch suitability	Non-parasitised fish consider predator density when during patch selection but is ignored by parasitised fish.
6	Aggregation of all parasite impacts (Direct & indirect loss of host energy) (Scenarios 1-5)	Simultaneous impacts on host territorial establishment and predator perception (Scenarios 4 & 5)	Accumulative modifications of reduced assimilation efficiency & reaction distance, increased swimming cost, processing order and fitness measure (Scenarios 1-5)	Impacts to host parameters set at 20%; parasitised fish are processed last; removal of predation risk during movement decisions by parasitised fish
7	Aggregation of all indirect parasite impacts that lead to host energy loss (Scenarios 2-5)	Simultaneous impacts on host territorial establishment and predator perception (Scenarios 4 & 5)	Accumulative modifications of & reaction distance, increased swimming cost, processing order and fitness measure (Scenarios 2-5)	Impacts to host parameters set at 20%; parasitised fish are processed last; removal of predation risk during movement decisions by parasitised fish

#### 5.2.3.1 Bioenergetic budgets (scenario 1)

Parasites can directly exploit host energy by consuming host proteins and/or carbohydrates and this creates an additional cost to the host that must be accounted for in their bioenergetic budget. The marine ectoparasite *Anilocra apogonae* has been observed to increase resting metabolic rates of hosts by up to 25% (Nilson et al. 2005). The extra energy expended by the host to maintain and feed parasite growth reduces the energy available to its own processes. The interaction in this scenario is modelled to affect host assimilation efficiency and infected hosts will have reduced assimilation efficiencies so less energy is available for host bioenergetic processes.

#### 5.2.3.2 Host sensory perception (scenario 2)

Parasite infection can affect the sensory ability of the host. Parasites that grow in the lens of the eye (e.g. *Diplostomum spathaceum*) can cause parasitic cataracts and eyefluke disease (Crowden & Broom 1980) and this will affect the vision of the host. In this scenario, parasitised fish have a lowered visual ability as a result have diminished reaction distances to invertebrate drift items.

#### 5.2.3.3 Locomotive efficiency (scenario 3)

Parasites can reduce the swimming performance by atrophy of musculature or nervous system and this interferes with the normal swimming movements of fish (Sweeting 1977) or by the obstruction of blood flow to muscles (Coleman 1993). Attachment by ectoparasites, damage to fins and scales can increase drag on the fish; sea lice have been recorded to decrease host salmonid swimming efficiency by up to 19% (Wagner et al. 2003). In this scenario, parasitised fish are simulated to have decreased locomotive efficiencies and this is modelled by raising the bioenergetic cost of host swimming activity.

#### *5.2.3.4 Competitive ability (scenario 4)*

A host's ability to compete for territory may be affected directly, through behavioural impacts, or indirectly through reduced physical ability brought about through physical costs associated with parasites (Barber et al. 2000). Scenario 4 tests the impact of reduced competitive ability by parasitised hosts and all parasitised fish are unable to compete against their non-parasitised conspecifics. This is modelled by altering the processing order of fish foragers in the IBM and in each timestep; non-parasitised fish are processed before parasitised fish in obtaining foraging territory.

#### *5.2.3.5 Predation boldness (scenario 5)*

Parasite infection can affect the antipredator behaviour ability of hosts. Milinski (1985) observed sticklebacks (*Gasterosteus aculeatus*) infected with a cestode parasite (*Schistocephalus solidus*) feeding closer than non-parasitised conspecifics to potential predators. In this scenario, this is modelled by removing predation risk when parasitised fish assess patch fitness.

#### *5.2.3.6 Aggregated direct and indirect impacts (scenario 6)*

Scenario 6 tests the impact on host growth and distribution when both direct and non-direct parasite impacts are impacting concurrently (i.e. all impacts described in scenarios 1-5). Parasitised fish in this scenario are impacted simultaneously with the impacts at the maximum percentages (20%) tested in their individual scenarios.

#### *5.2.3.6 7 Aggregated indirect impacts (scenario 7)*

Scenario 7 investigates the effect of indirect energy loss by parasite infection on salmonid population (i.e. the energy lost by an infected host by pathways other than direct consumption from parasites). This was modelled by parasitised fish simultaneously impacted by scenarios 2-5 with the omission of direct energy loss by direct consumption by parasites (scenario 1).

#### 5.2.4 Measuring population patterns

##### *Specific growth rates*

The growth rates of foragers are calculated in terms of specific growth rates or the percentage change in body mass per day (% day<sup>-1</sup>). This is expressed as:

$$SGR = \frac{\ln(W_{salmonid\ t_n}) - \ln(W_{salmonid\ t_0})}{t_n - t_0} * 100$$

Where SGR is the specific growth rate,  $W_{salmonid\ t_0}$  is the initial mass at tagging ( $t_0$ ) and  $W_{salmonid\ t_n}$  is the mass at recapture and  $t_n - t_0$  is the number of days between recapture.

##### *Fish distribution by the environmental characteristics of the patch they occupy*

Patch selection by parasitised and non-parasitised fish is classified by the velocity and depth characteristics of the patch they occupy. A patch is a unit of area ( $39.6 \pm 14.1\text{m}^2$ , mean  $\pm$  s.d.) of homogenous characteristics in the modelled environment (see chapter 2 for a detailed description of environmental characteristics). The patch occupancy of fish is observed at nine points (timesteps) during a model simulation. These timesteps correspond to tracking events used for model validation (see Chapter 3).



*Fish population distribution at the stretch level*

The ‘macrohabitat distribution’ is a measure of the distribution of foragers in the model environment expressed as the forager population within a stretch as a proportion of the total population. A stretch is a consecutive run of relatively environmentally similar patches (see chapter 2). The distribution of parasitised fish and non-parasitised fish are calculated independently of each other. Macrohabitat distribution is measured as relative proportions per stretch and is calculated as:

$$Proportion_{stretch,i} = \frac{no. individuals in stretch_i}{total no. individuals in stretch_{all}}$$

Where  $i$  = the stretch being analysed and  $all$  = all the stretches considered in the analysis.

## 5.3 Results

### 5.3.1 Physical impacts – Scenarios 1- 3

The growth rates of parasitised young-of-year (YoY) Atlantic salmon and brown trout have a differential response to the type of physical parasite impact (Figure 5.1). Infected fish under a scenario of direct parasite consumption of host energies (scenario 1) show a linear decline in growth rates with increasing intensity of parasite impact. A parasitic cost of 15% (circa) assimilated energy is sufficient to reduce salmonid growth rates to zero and costs above this will lead to the host losing weight. The growth rates of parasitised salmonids with reduced reaction distances or increased swimming costs associated with parasite infection (scenario 2 & 3) do not show significantly reduced growth rates even under high intensities (ANOVA,  $p>0.05$ ).

### 5.3.2 Behavioural impacts – Scenarios 4 & 5

Behavioural impacts on growth rates of parasitised fish show a mixed response (Figure 5.2). Parasitised fish that have altered perception of predation risk (i.e. modified fitness measure – scenario 5), are predicted to have a significantly higher mean growth rate; parasitised Atlantic salmon grew at 1.18%  $\text{bodymass.day}^{-1}$  whilst non-parasitised conspecifics grew at 1.09%  $\text{bodymass.day}^{-1}$  (t-test,  $p<0.05$ ) and parasitised brown trout grew at 0.98%  $\text{bodymass.day}^{-1}$  whilst non-parasitised conspecifics grew at 0.92%  $\text{bodymass.day}^{-1}$  (t-test,  $p<0.05$ ). Conversely, parasitised fish that have an affect of reduced dominance ability (scenario 4) have lower mean growth rates than their non-parasitised conspecifics; parasitised Atlantic salmon grew at 1.07%  $\text{bodymass.day}^{-1}$  whilst non-parasitised conspecifics at 1.22%  $\text{bodymass.day}^{-1}$  (t-test,  $p<0.05$ ) and parasitised brown trout grew at 0.91%  $\text{bodymass.day}^{-1}$  whilst non-parasitised conspecifics at 1.00%  $\text{bodymass.day}^{-1}$  (t-test,  $p<0.05$ ).

### *5.3.3 Aggregated impacts – simultaneous physical and behavioural impacts (Scenarios 6 & 7)*

Modelled growth rates of parasitised fish subject to accumulative direct and indirect impacts (scenario 6) and just indirect impacts (scenario 7) were predicted to be lower than non-parasitised conspecifics (Figure 5.3). Parasitised fish in scenario 6 showed a large decline in growth rates with some individual fish exhibiting no growth over the simulated period at parasite impacts above 10% with some fish experiencing negative growth at higher percentage impacts. The impact under scenario 7 on parasitised fish was not as severe as under scenario 6 with growth rates of parasitised fish on average 30% less than non-parasitised fish – but still displayed positive growth rates at all parasite impacts modelled.

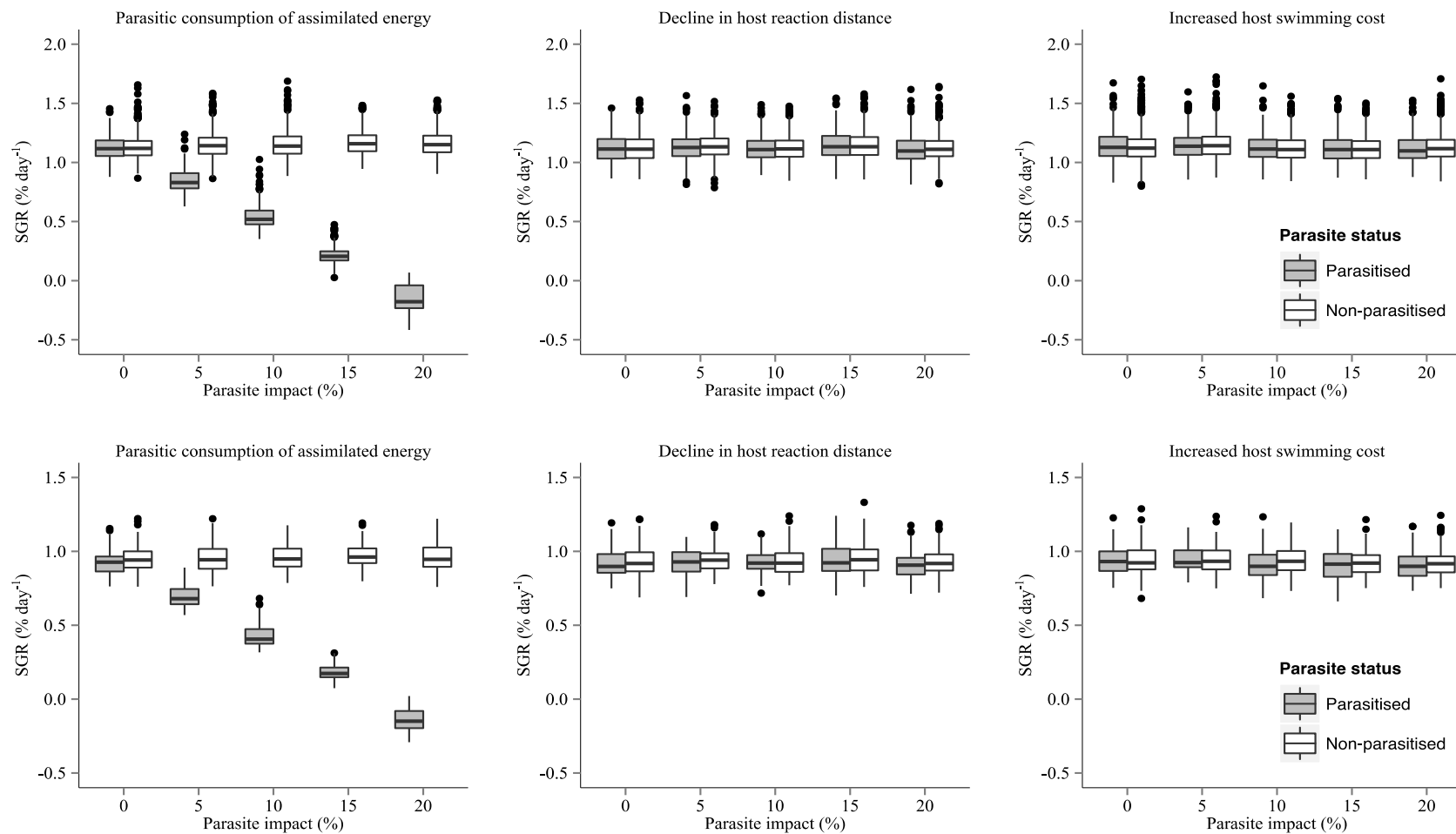


Figure 5.1 The specific growth rates (SGR) of parasitised and non-parasitised on two species of young-of-year (YoY) salmonids; Atlantic salmon (*Salmo salar*) - top row and brown trout (*Salmo trutta*) - bottom row. The impact of parasitism is modelled with varying intensities of different parasite-host interactions (i.e. scenarios 1-3).

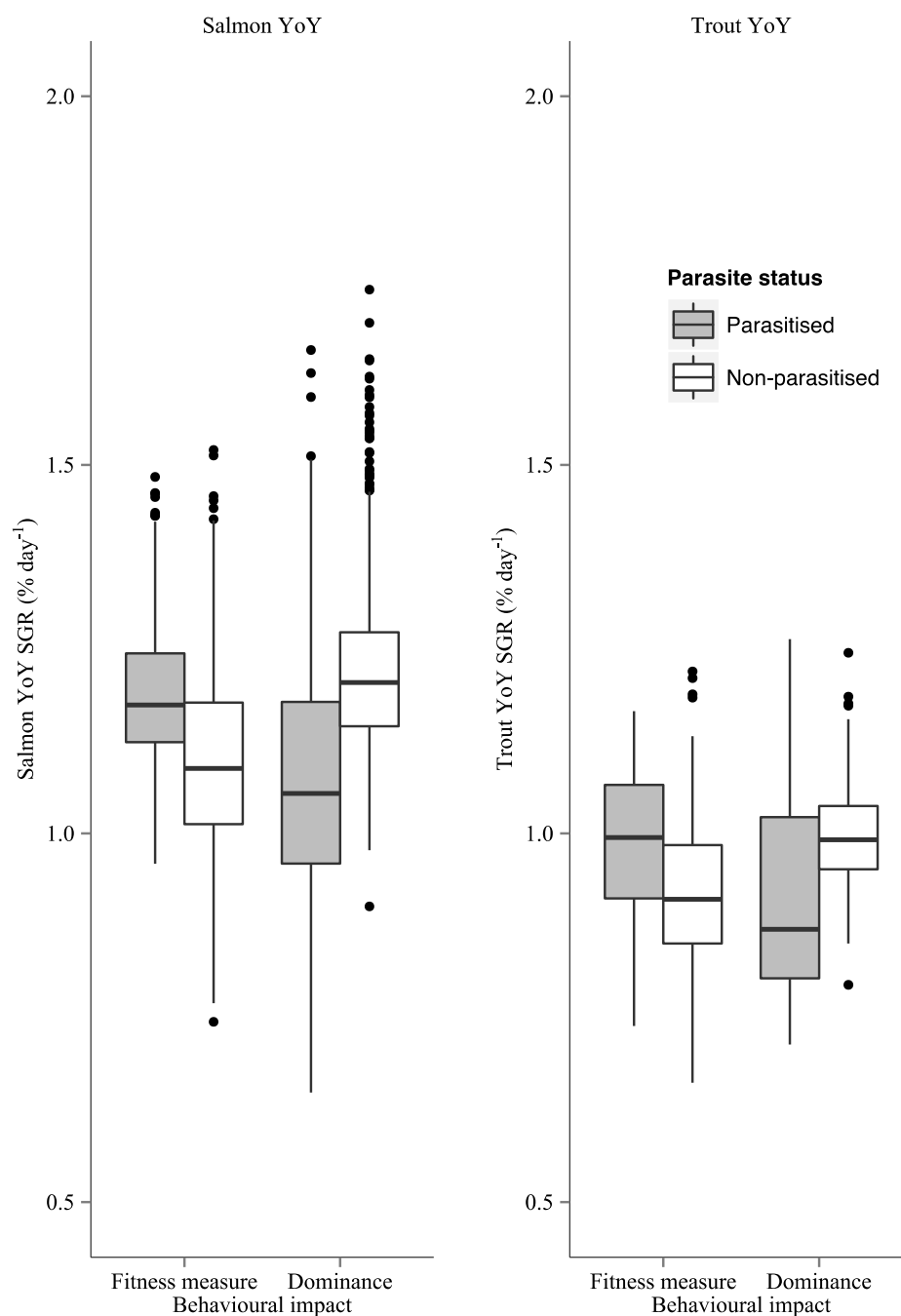


Figure 5.2 Predicted growth rates of parasitised and non-parasitised young-of-year salmonids, Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) under different infection impacts; parasitised hosts have reduced competitive ability against non-parasitised conspecifics ('dominance', i.e. scenario 4) or ignore the risk of predation during patch selection ('fitness measure', i.e. scenario 5).

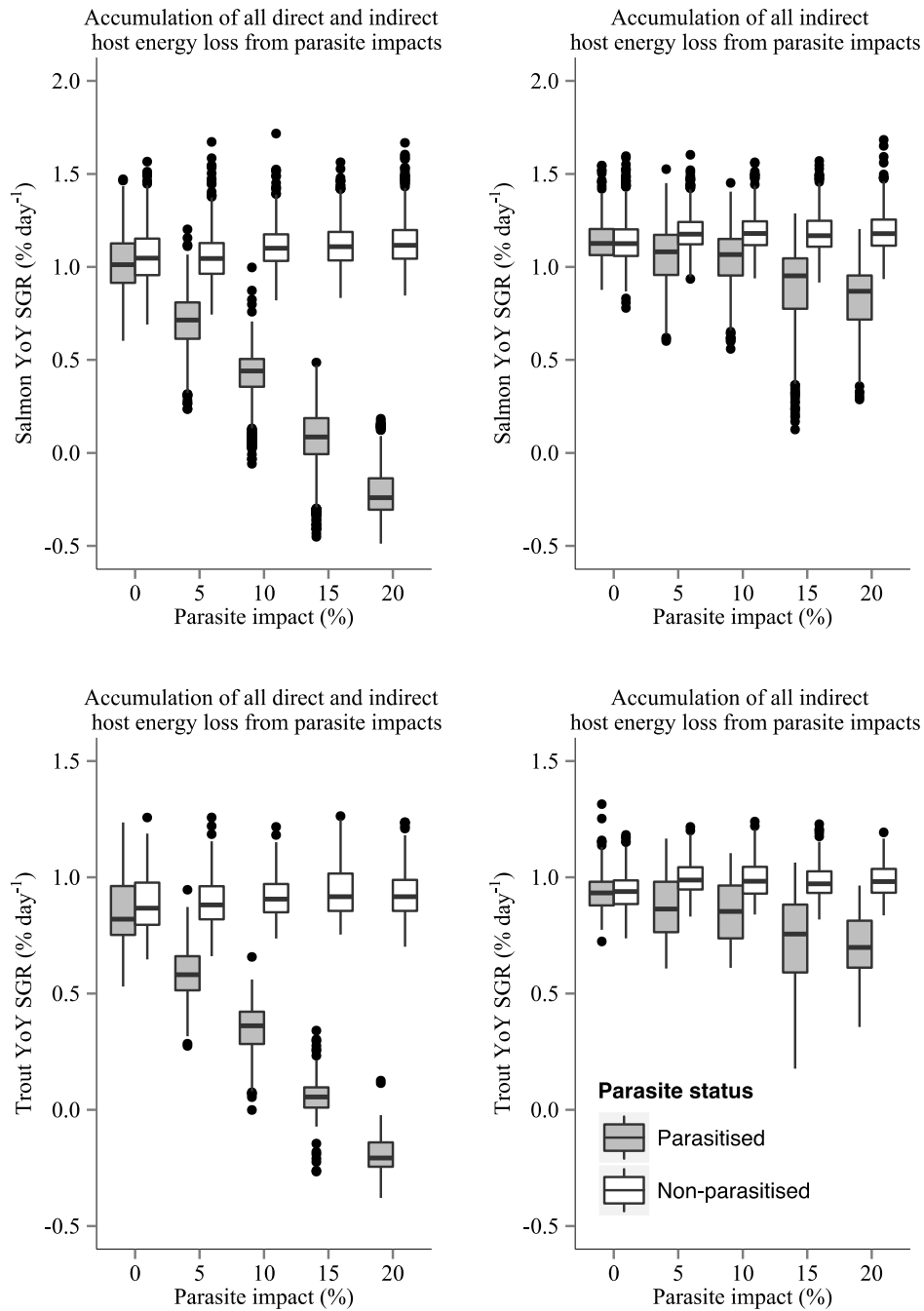


Figure 5.3 Predicted impacts on the growth rates of young-of-year salmonids, Atlantic salmon (*Salmo salar*) – top row and brown trout (*Salmo trutta*) – bottom row, under two scenarios of parasite-host impacts. Scenario 6 - *left column*; parasitised fish are subject to both direct (consumption of host energy) and indirect parasite impacts host energy reserves (reduced visual prey capture distance, increased costs associated with swimming, reduced competitive ability against non-parasitised hosts and reduced awareness of predators). Scenario 7 – *right column*; parasitised fish are just subjected to the indirect effects of parasitism.

#### *5.3.4 Fish distribution patterns*

Parasitised and non-parasitised fish show differential preference for patch depths and velocities (Figure 5.4). Parasitised YoY Atlantic salmon show a similar preference for patch depth and velocity as non-parasitised fish with the exception of parasitised fish with reduced competitive ability (reduced dominance) showing an increased occupancy of patches with greater depths than the patches selected by non-parasitised fish. The differences between parasitised and non-parasitised YoY brown trout show a much more varied response in patch characteristics than YoY Atlantic salmon, but are still very similar. For both behavioural impacts, there is a preference for parasitised brown trout to select patches with lower velocity but higher depths than non-parasitised fish and the differences show a greater discrepancy with time.

The difference in patch habitat preferences between non-parasitised and parasitised conspecifics resulted in a change in spatial distribution (Figure 5.5) at the level of the stretch; there was an increase in the use of stretch 4 and stretch 7, facilitated by a decrease in the use of stretch 3 and 6. A reduction in dominance ability of parasitised fish (scenario 4) led to a more even distribution across the stretches; parasitised fish showed greater occupancy in stretches that non-parasitised fish avoided (stretches 1, 4, 5 & 6) and a reduced occupancy in the stretches favoured by non-parasitised fish (stretches 2 & 3). Stretch 7 showed greater occupancy by parasitised fish even though non-parasitised fish favoured this stretch. These changes in spatial distribution was observed in both YoY Atlantic salmon and YoY brown trout with the exception that brown trout avoided stretch 5 in all scenarios whilst Atlantic salmon would show some, albeit very minimal, occupancy. Parasitised fish with physical impacts from parasitism (scenarios 1, 2 & 3) did not exhibit a difference in stretch distribution when compared with their non-parasitised conspecifics.

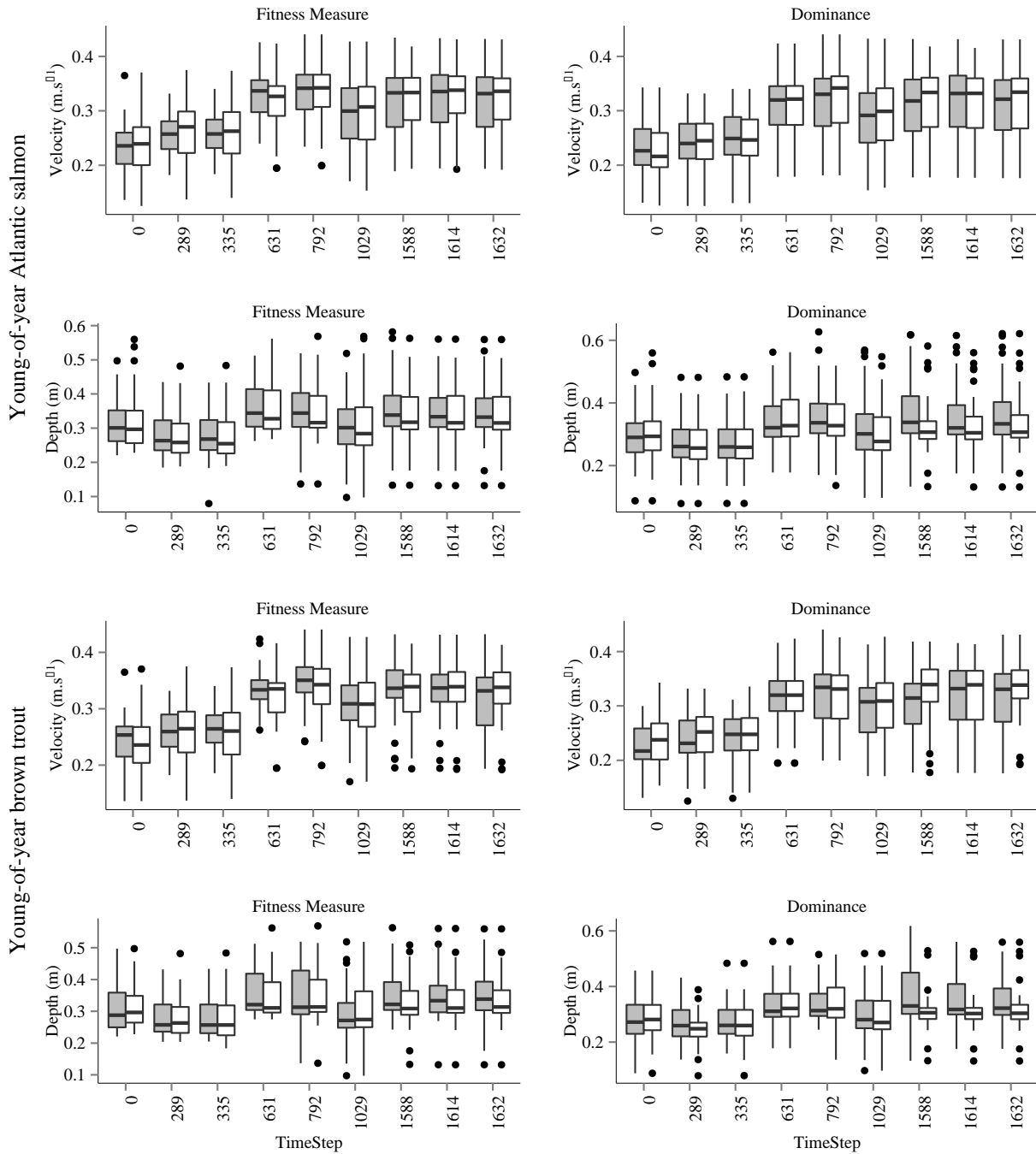


Figure 5.4 The patch characteristics (water velocity and depth) of the patches occupied by parasitised (grey) and non-parasitised (white) young-of-year (YoY) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*). The impact of parasite infection are i) to ignore the risk of predation when selecting a patch ('fitness measure, i.e. scenario 5) or ii) reduce the intraspecific competitive ability of the infected host ('dominance', scenario 4).



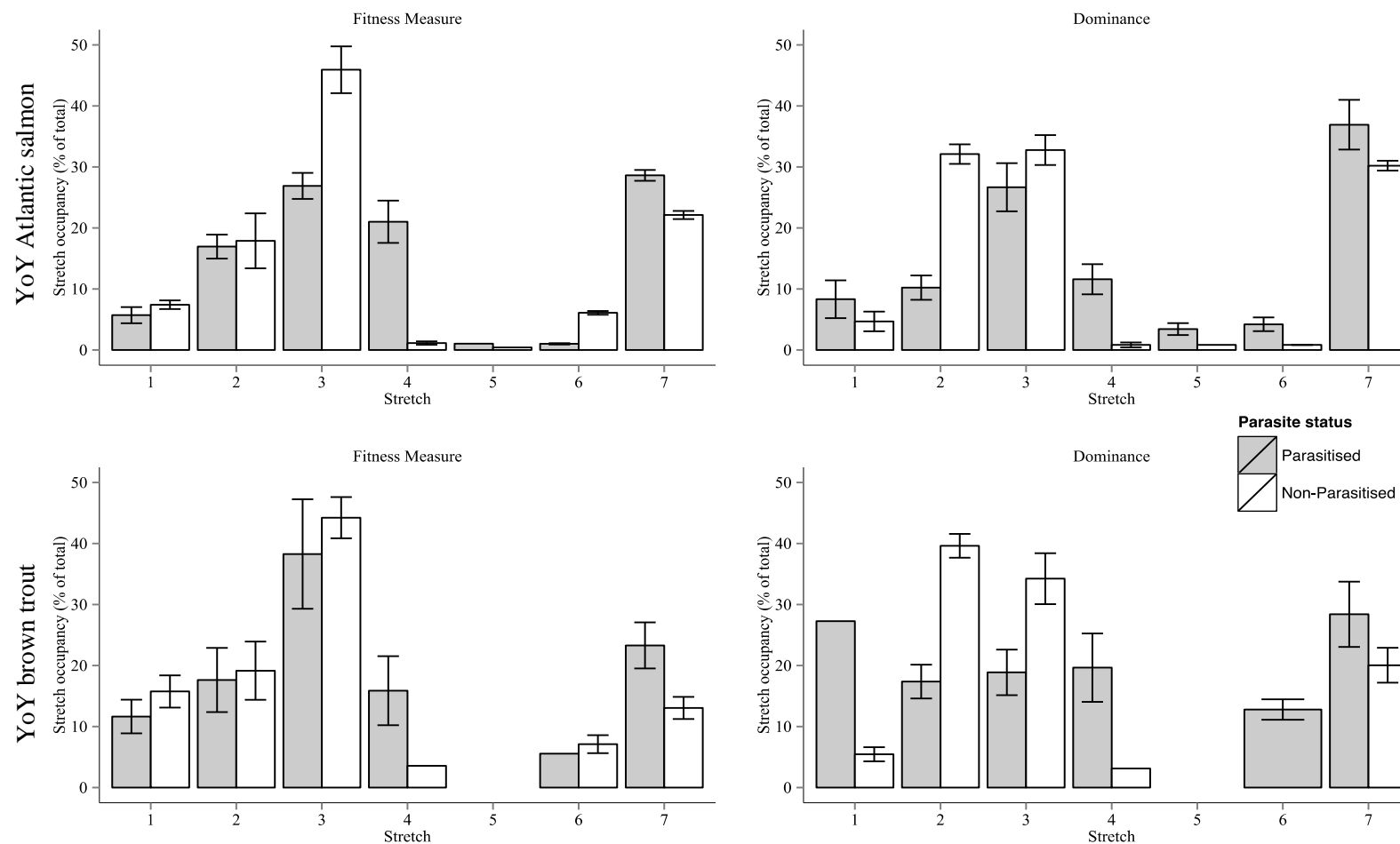


Figure 5.5. The predicted distribution of parasitised and non-parasitised young-of-year salmonids across the modelled site, Atlantic salmon (*Salmo salar*) and brown trout (*Salmo salar*). The impact of parasite infection are i) to ignore the risk of predation when selecting a patch ('fitness measure', i.e. scenario 5) or ii) to reduce the intraspecific competitiveness of the infected host fish with non-parasitised conspecifics ('dominance', i.e. scenario 4).

## 5.4 Discussion

The model predicts that the pathway of impacts affecting young-of-year Atlantic salmon and brown trout growth rates, from most to least impactful, are: direct consumption of host energy (scenario 1), reduced intraspecific competitive ability/dominance (scenario 4), increased swimming costs (scenario 3) and reduced reaction distance to drifting prey items (scenario 2). Parasite-induced host behavioural change of reduced competitive ability with conspecifics and reduced predation awareness showed a mixed impact on parasitised host growth rates with the former effect having a negative impact on growth rates (parasitised fish grew less) whilst the latter had the opposite effect (parasitised fish grew more). When the impacts are modelled as an accumulative effect on parasitised salmonids, the effect is a greater negative impact on growth rates than when the impacts are modelled independently. Parasite infection can also manipulate the distribution of fish within the system as impacts on host behaviour with parasite impacts on host perception of predation risk and intraspecific competitive ability causing parasitised fish to distribute themselves to different velocities and depths resulting in a different spatial pattern at a larger scale. Management need to consider these results and prioritise the implementation of regimes that prevent the introduction or spread of parasites that consume salmonid fish energy over parasites that affect the visual ability of the host.

Compared to parasites that affect host swimming efficiency or limit prey detection distance, parasites that impact directly on the energetic budget of their host resulted in the largest decrease in host growth with decrease of up to 30% when compared to non-parasitised host. Examples of fish parasites that directly consume host energy include *Schistocephalus solidus* (Schulz et al. 2006) and *Apophallus brevis* (Johnson & Dick 2001). Such parasites can grow at rates up to 70% dry mass increase per week and such high parasite growth will represent a significant bioenergetic cost to the host (Meakins & Walkey 1973; Meakins & Walkey 1975). As YoY salmonid

overwinter survival is closely related to bodymass and hence growth rates (Quinn & Peterson 1996; Hunt 1969), parasite-induced low growth rates will lead to increased mortality of hosts with infected by energetic budget impacting parasites (Francova & Ondrackova 2013). The high productivity of the modelled environment must be considered as this may have limited the effect on hosts infected by parasites that impact swimming cost and/or reduced reaction distances to prey. In effect, invertebrate densities in chalk streams are very high (Wright & Symes 1999), especially during the summer months (the period modelled). Whilst a reduction in host reaction distance would lower forager capture window, the densities of preys in the system may be sufficiently high that there is very little overall impact on the total amount of food consumed. High resource densities also mean less energy spent on foraging activities as total time spent foraging is not severely impacted. The predicted limited impact these types of parasites have on infected salmonids may only be applicable in habitats with high densities of drifting invertebrates and a greater effect may be seen in habitats that are resource poor.

Whilst most parasitic impacts resulted in negative salmonid growth and distribution, the parasitic change in host boldness (reduced attention to predation risk) led to an increase in salmonid growth rates. Larger YoY salmonids have higher rates of survival (especially overwinter survival - Quinn & Peterson 1996; Hunt 1969) and parasite infection of YoY salmonids may result in a reproductive fitness advantage. This is an interesting insight on the role parasites may have on host evolution and temporal gene flow within a population (Hochberg et al. 1992). However, any benefit from increased growth rates may be offset as reduced host attention predation risk might also lead to increased rates of mortality due to predation; predators select against faster growing and risk taking behaviour in another salmonid, brook trout (*Salvelinus fontinalis*) (Biro et al. 2004). Predation and parasite infection are interactions that affect the evolution of each other as well as the evolution of the host (Choo et al. 2003).

The result of increased host growth due to parasite infection affecting host predator perception provide an alternative pathway than shown in Ballabeni (1995) where parasitised hosts were observed to grow larger than non-parasitised hosts due to phenotypic trait adaptive response to infection. The results here show that indirect parasite impacts on behaviour might be an alternative mechanism that might cause increased host growth. Parasitised hosts may be growing larger as a result of the impact of infection as opposed to adaptive response to it; the difference is subtle but important as the direction of the process differs.

In Barber et al. (2000) review of parasites on fish behaviour, they highlight the difficulty in separating between indirect and direct manipulation of host behaviours without detailed and resource intensive studies. Whilst understanding the precise mechanisms by which infections impact host behaviours would help understand the host-parasite relationship (Poulin 1995), the methodology used here does not require such detailed information and can assess risk by type of impact. Overcoming such limitation in our prediction of parasitic impact on host population is one advantage of the approach of individual-based models that can be used to understand population responses under novel environments (Stillman et al. 2000). This is the first time that they are used to test the effect of parasite introductions at population level and along with investigations on the modes of parasite spread and introduction (e.g. Peeler et al. 2011) such models can provide additional decision-making tools for environmental managers. These findings can be used as a fast approach to quantifying predicted parasite impacts on a host population and will help to assist in the prioritisation of parasite risk. Management could start drawing a map of high impact parasites based on their effect on infected hosts; parasites heavily reliant on host food resources and that diminish that ability of salmonid hosts to compete will have the greatest impacts and management should divert resources and focus on preventing their introduction.

Conversely, fewer resources should be spent on managing parasites that are superficial ectoparasites that are less draining on host-assimilated energy, as their impacts are less. Investigations in to specific parasites have concluded that not all parasites are predicted to have a significant negative impact on infected hosts or their population (Pegg et al. 2011).

Parasites and associated impacts are an increasing risk factor as increased global connectivity have introduced non-native parasites to previously uninfected systems and have the potential to cause serious negative population results (Daszak et al. 2000, Arsan & Bartholomew 2009; Gozlan et al. 2006). Parasite monitoring and research should not be done on a reactive basis as management intervention may be too delayed by the time it is discovered in previously uninfected populations (McCallum & Dobson 1995). Scientists need to provide tools for an evidence-based approach to managing parasite risk and there is potential for the approach adopted here to assist by providing information to prioritise resource allocation for effective proactive management to threats.

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## **6. Incorporating salmonid behaviour into aquatic macrophyte management**

### **6.1 Introduction**

The degradation and fragmentation of freshwater riverine habitats is a major threat to the future of fish populations (Dudgeon et al. 2006). The distribution and health of salmonid populations is influenced by the riverine habitat (Armstrong et al. 2003) and the degradation or loss of habitat will have a negative impact on the population. In English chalk stream ecosystems, the dominant in-stream macrophytes are a group of around 200 species in the *Ranunculus* genus (Flynn et al. 2002). The growth of aquatic macrophytes plays an important role in riverine habitats as a source of primary productivity, physical habitat and influencing local hydrology (Gregg & Rose 1982). However, *Ranunculus spp.* growth can be so dense as to increase risk of flooding and is consequently removed (Dawson 1979). Whilst there may be just cause for *Ranunculus spp.* Removal, it is pertinent to understand the effects such a significant habitat management regime has on local salmonid populations.

The typical structure of *Ranunculus spp.* is that of a ‘plume’ shape; with roots anchoring in the riverbed upstream and vascular growth being pulled down stream by river flow, with several plants growing together to form a stand (Dawson 1979). The stands engineer the chalk stream habitat by affecting river flow and improve water quality by trapping suspended sediments resulting in clear, low water turbidity (Madsen et al. 2001). In the warm and high sunlight summer months, *Ranunculus spp.* stands can grow substantially large and dense, modifying local flow characteristics (i.e. the high surface resistance by plant structure retards the speed of water flow in the channel and increases water retention) which results in an increased flood risk (Gregg & Rose 1982) and stands are cut to mitigate this risk (Dawson 1979). Additionally, stands may also be cut to reduce the aquatic cover in a stretch to increase fishing access. However, such drastic changes

in the biomass of the dominant chalk stream aquatic macrophyte will have knock on effects on organic input and habitat for other plants and animals (Wharton et al. 2006).

The growth of *Ranunculus spp.* creates heterogeneity in flow velocity and depth and these microhabitats are utilised by salmonids for different purposes including but not limited to activities such as cover, feeding and velocity shelters (Hayes & Jowett 1994; Degraaf & Bain 1986; Heggenes et al. 1996). Despite the value of chalk stream salmonid fisheries, there have been limited studies investigating the effect the removal of *Ranunculus spp.* has on salmonid populations (but see Roussel et al. 1998 and Riley et al. 2009). Roussel et al. (1998) observed that the removal of *Ranunculus spp.* led to an overall decrease in fish numbers but numbers of Atlantic salmon (*Salmo salar*) actually increased after removal. However, their study only recorded absolute fish numbers and makes no reference to fish size, raising questions as just using overall population numbers is not a reliable proxy for population health (see chapter 4). One particular use of the habitat *Ranunculus spp.* provides by fish is as a refuge to avoid predators. Pickering et al. (1987) showed that in the absence of overhead cover, salmonid fish had significantly increased levels of stress and this resulted in reduced growth rates. Thus, with salmonid survival rates linked to body mass (Murphy et al. 2006), it can be hypothesised that the removal of *Ranunculus spp.* stands and the cover they provide would negatively affect salmonid population health.

Whilst there may be a legitimate need for the management of *Ranunculus spp.*, the potential impact on economically important salmonid stocks needs to be addressed with the current understanding being unclear. The aim of this chapter is to use the previously validated salmonid IBM developed in chapter 3 to characterise the importance of *Ranunculus spp.* on salmonid individual growth and distribution to help design salmonid-sympathetic removal regimes.

## 6.2 Methodology

### 6.2.1 *The virtual environment*

Observations of environmental parameters and fish population responses to the removal of *Ranunculus spp.* stands were carried out in the period from June 2010 to October 2010. This data on both the environmental conditions and fish population parameters were used to parameterise the virtual environment and the population characteristics of salmonids in the salmonid IBM as described in chapter 3. See chapter 2 for detailed description of environmental conditions of the 2010 environment and complimentary information about particular fieldwork methodologies used to record them.

### 6.2.2 *Fieldwork*

#### *Mill Stream aquatic macrophyte removal*

All growth of the main in-stream weed, *Ranunculus spp.*, was removed from the channel by cutting over a three-day period prior to environmental recording. *Ranunculus spp.* stands were cut ten centimetres (circa) above the substrate and was removed from the channel. *Ranunculus spp.* was the dominant aquatic macrophyte species but other aquatic macrophyte strands that were found within the main channel were removed as well. HABSCORE assessments of each patch provided the physical patch characteristics for parameterisation of the virtual habitat. Bankside vegetation was not managed and fish populations were not manipulated.

#### *Environmental and fish populations*

The response in salmonid population growth and distribution was recorded by four electric fishing surveys (see chapter 2). The size structure and relative abundance of invertebrate drift per stretch was estimated from monthly drift net sample surveys; a total of three survey days (once a month) and a sample were taken at three times per day (dawn, mid-day and

dusk) (see chapter 2 for drift net sampling methodology). Given known sampling errors in using drift nets to estimate drift densities, the final drift densities were calculated by multiplying estimates of drift densities from the drift net samples by the stretch's correction coefficient calculated from the surveys of drift and benthic invertebrate abundance collected in 2008 (see chapter 2 and 3). Temperature and discharge measurements readings were recording by observational stations operated by the Game and Wildlife Conservation Trust and Environment Agency respectively (see chapter 2).

### *6.2.3 Model parameterisation*

#### *Spatial extent of the virtual environment*

The virtual environment consists of the same stretch of river as the model described in chapter 3. The same delineations of total length, stretch and patch are used and the modelled system is representative of a closed system.

#### *Global parameters*

The global parameters of timestep, daylight hours, discharge and water temperature are parameterised from recordings of the environment in the Mill Stream in 2010 (see chapter 2). Salmonid bioenergetic energy remains the same (see chapter 3).

#### *Stretch resource density*

Drift density is estimated from drift net samples collected in 2010 and stretch-specific Correction Coefficient estimated from samples (both drift and benthic drift invertebrate densities) collected in 2008. A linear regression is used to estimate densities in the timesteps between sampling points (i.e. the timesteps between estimated densities at dawn to midday and midday to dusk). A linear regression is also used to estimate the daily change in drift densities between sample dates. The same size structure of drift densities is used (1-3; 3-5; 5-7; 7-9; 9-12 mm) and drift densities at night are assumed to be zero.

### *Patch velocity & depth*

Access to the 1-D hydrological model (see chapter 3) was not available to estimate mean patch velocity ( $\text{m.s}^{-1}$ ) and depth (m) per timestep. These are estimated using discharge measurements and patch specific discharge~velocity and discharge~depth relationships using predictions from the 1-D hydrological model calibrated on 2008 data. The hydrological model predicting patch depth and velocity is used to calculate linear models of discharge~velocity and discharge~depth relationships from the period of reduced flow (see chapter 2). The Mill Stream environment in that period most closely matched the environment in 2010 as aquatic cover was low due to natural *Ranunculus spp.* dieback and discharge was similar. To calculate the relevant linear models the following equations were used:

$$Vel_{Pi(2008)} = a_{Pi2008} * Dis_{Pi(2008)} + b_{Pi2008}$$

Where *Vel* is velocity, *Dis* is discharge, *P* is patch and *i* is its identifier. *a* and *b* are constants defining the linear relationship between patch velocity and discharge.

$$Dep_{Pi(2008)} = a_{Pi2008} * Dis_{Pi(2008)} + b_{Pi2008}$$

Where *Dep* is depth, *Dis* is discharge, *P* is patch and *i* is its identifier. *a* and *b* are constants defining the linear relationship between patch velocity and discharge.

Velocity and depth estimates for patches in 2010 were calculated using recorded discharge measurements (see discharge subsection) using the following equations:

$$Vel_{Pi(2010)} = a_{Pi2008} * Dis_{Pi(2010)} + b_{Pi2008}$$

Where *Vel* is velocity, *Dis* is discharge, *P* is patch and *i* is its identifier. *a* and *b* are constants defining the linear relationship between patch velocity and depth calculated from 2008 data.

$$Dep_{Pi(2010)} = a_{Pi2008} * Dis_{Pi(2010)} + b_{Pi2008}$$

Where *Dep* is depth, *Dis* is discharge, *P* is patch and *i* is its identifier. *a* and *b* are constants defining the linear relationship between patch velocity and depth calculated from 2008 data.

#### *Virtual forager types*

There are no changes to the forager types in this model which are the same as described in chapter 2. There are 84 forager types and are defined by the i) species (Atlantic salmon or brown trout), ii) starting stretch, (1-7) iii) age (YoY, 1+, 2+ or 3+) and iv) if the fish is ‘tagged’ (tagged or untagged). The number of foragers per forager type is based on the number of caught fish on the first electric fishing survey in 2010 (chapter 2). Starting bodymass for each forager type is drawn from a normal distribution from bodymass data from the same electric fishing survey. No changes were made to the submodels defining fish feeding or bioenergetics.

### *Stress parameter*

A stress parameter is introduced into this model and this was not present in the model as described in chapter 3. Atlantic salmon and brown trout display stressed behaviour in the absence of overhead cover but the extent that they are affected differs (Pickering et al. 1987) so two ‘stress’ parameters need to be calibrated ( $S_{\text{Atlantic salmon}}$  and  $S_{\text{brown trout}}$ ). Stress has been observed to affect fish consumption (Gregory & Wood 1999) and the species-specific stress parameters are incorporated by the following transformation of forager maximum consumption rates ( $C_{\text{max}}$ ). In the presence of overhead cover, fish are not subjected to stress and  $S_{FS} = 0$  for both species.

$$C_{\text{max}_{FS, \text{actual}}} = \frac{1 - S_{FS}}{1} * C_{\text{max}_{FS, \text{theoretical}}}$$

Where  $C_{\text{max}_{\text{actual}}}$  is the maximum consumption by the forager,  $S$  is the species-specific calibrated stress parameter,  $FS$  is the fish species (Atlantic salmon or brown trout) and  $C_{\text{max}_{\text{theoretical}}}$  is the maximum consumption rate as defined in chapter 3 (the maximum energy consumed per daylight hour adapted from Elliot 1976a).

The submodels defining forager bioenergetics ( $C_{\text{max}}$ ,  $R_{\text{stand}}$ ,  $R_{\text{digestion}}$ ,  $SC_{\text{feeding}}$  &  $SC_{\text{resting}}$ ) and territory size are untouched and remain the same. See Chapter 3 for detailed description.



### *Fitness rule*

The fitness rule is modified to incorporate fish adaptive behaviour in response to aquatic cover. The fitness rule still follows an optimal foraging approach as it incorporates both consumption rates and predation risk but accounts for the impact stress parameter has on  $C_{\text{max}_{\text{actual}}}$  in patches according to their overhead cover. The threshold value of aquatic cover, above which a forager's consumption  $C_{\text{max}}$  is not impacted (i.e. no stress or  $S = 0$ ), is arbitrarily at 1% of patch area; if aquatic cover  $> 0.01$ , the fish were unstressed and  $C_{\text{max}_{\text{actual}}}$  equalled  $C_{\text{max}_{\text{theoretical}}}$ . With no collected data to estimate the minimum required macrophyte cover before salmonids exhibit no stress, the threshold was set as purposefully low at a very conservative 1%. Fish calculate the fitness of each patch at each timestep using the fitness rule and select the patch with the highest fitness.

The fitness rule consists of three steps:

1. Selection of the patch which provides the largest  $C_{\text{max}_{\text{actual}}}$ ,
2. If rate of consumption achieves  $C_{\text{max}}$ ;
  - a. predation risk is considered and select behaviour that minimises predation risk.

If rate of consumption does not achieve  $C_{\text{max}}$ ;

- b. predation risk is unaccounted for and select behaviour that maximises consumption
3. It is assumed that predation risk is equal for all individuals vulnerable to the respective predator sizes. Predation risk is calculated at the patch level as:

$$PR_i = \frac{PD_i}{VI_i}$$

Where  $PR$  = predation risk,  $PD$  = predator density,  $VI$  = number of foragers vulnerable to predation and  $i$  = patch number.

## 6.2.4 Model analysis and calibration

### *Forager class*

Analysis of model performance is calculated by comparing model predictions against observed patterns of real fish collected during fieldwork. Whilst the model classifies foragers by forager types, these are aggregated into forager classes during analysis. A forager class is the collection of foragers types of the same species (Atlantic salmon or brown trout) but distinguished by age (YoY, 1+, 2+, 3+) (see chapter 2 and 3).

### *Specific growth rates*

The growth rates of foragers are calculated in terms of specific growth rates or the percentage change in body mass per day (% day<sup>-1</sup>). This is expressed as:

$$SGR = \frac{\ln(W_{salmonid\ t_n}) - \ln(W_{salmonid\ t_0})}{t_n - t_0} * 100$$

Where SGR is specific growth rate,  $W_{salmonid\ t_0}$  is the mass at the start of the period ( $t_0$ ) and  $W_{salmonid\ t_n}$  is the mass at the end of the period and  $t_n - t_0$  is the number of days between recapture.

### *Forager population distribution at the stretch level (macrohabitat)*

The ‘macrohabitat distribution’ is a measure of the distribution of foragers in the model environment expressed as the forager population within a stretch as a proportion of the total population. Some stretches were omitted when comparing model distribution and distributions collected during fieldwork due to poor depletion during electrofishing of a stretch leading to high variance when estimating stretch population density; resulting in low confidence in population density estimates.

Macrohabitat distribution is measured as relative proportions per stretch and is calculated as:

$$Proportion_{stretch,i} = \frac{no. individuals in stretch_i}{total no. individuals in stretch_{all}}$$

Where  $i$  = the stretch being analysed and  $all$  = all the stretches considered in the analysis.

#### *Calibration of stress parameters $S_{Atlantic\ salmon}$ and $S_{brown\ trout}$*

The two parameters,  $S_{Atlantic\ salmon}$  and  $S_{brown\ trout}$ , are calibrated by comparing predicted and observed growth rates of their respective species for two periods (August-September and September-October). The normalised root-mean squared deviation (NRMSD) is used to measure the distance between predicted and observed patterns (Kobayashi & Salham 2000; Kramer-Schadt et al. 2007; q et al. 2003). NRMSD values were calculated as:

$$NRMSD = \frac{\sqrt{\sum_{i=1}^n (x_{obs,i} - x_{pred,i})^2}}{(max(x_{obs}) - min(x_{obs}))}$$

Where NRMSD is normalised root-mean, square-deviation,  $\chi_{obs}$  is the observed specific growth rate of a forager,  $\chi_{pred}$  is the predicted specific growth of the forager,  $n$  is the total number of observed specific growth rates of that forager type.

For each forager class (YoY Atlantic salmon, YoY brown trout, 1+ brown trout), a mean NRMSD value was calculated for each period. Each forager class and month was given the same weighting and the sum total NRMSD was used to measure the difference between observed and predicted patterns for values of  $S_{Atlantic\ salmon}$  and  $S_{brown\ trout}$ . The set of  $S_{Atlantic\ salmon}$  and  $S_{brown\ trout}$  with the lowest total NRMSD gives the predicted pattern that most closely predicts observed patterns.

#### 6.2.5 Validation

The calibrated model is validated by comparing the predicted spatial distribution patterns of foragers against the observed distribution of real fish distributions recorded from fieldwork. Predicted proportions are plotted against observed proportions and the estimated linear regression for that relationship is statistically tested against a perfect prediction relationship of a slope of 1 with an intercept at (0,0). The t-value of the difference gradient ( $\text{slope}_{\text{relationship}}$  vs. 1) and intercept ( $\text{intercept}_{\text{relationship}}$  vs. 0) is used to calculate the probability of difference in a two-tailed evaluation.

#### 6.2.6 Scenario testing

Two scenarios of weed cover were tested using the calibrated model; 1) natural *Ranunculus spp.* cover and 2) *Ranunculus spp.* cover after removal. The distribution of *Ranunculus spp.* for both scenarios reflected HABSCORE measured cover of aquatic vegetation per patch under their respective weed management scenarios of the field site in 2008 and 2010 respectively. Cover was assessed as a percentage area of the patch where *Ranunculus spp.* was present and does not infer structural complexity or size of the stand.

## 6.3 Results

### 6.3.1 Calibration – specific growth rates

The parameters of  $S_{\text{Atlantic salmon}}$  and  $S_{\text{brown trout}}$  that produced the lowest NRMSD when comparing predicted and observed SGRs was 0.13 and 0.07 respectively (Figure 6.1).

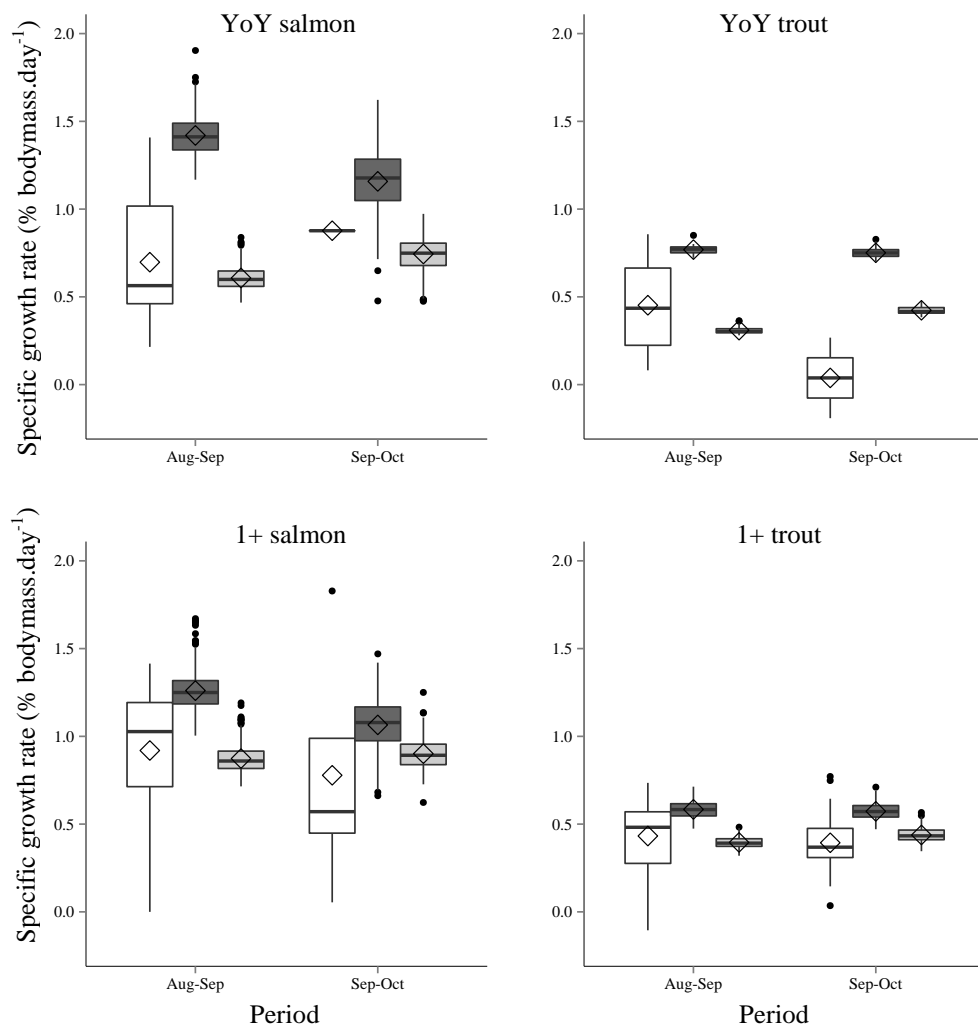


Figure 6.1 The observed and predicted growth rates of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) under a treatment of *Ranunculus spp.* removal; observed growth rates from the fieldwork study (white), uncalibrated salmonid individual-based model (IBM) (dark grey) and calibrated model (light grey). The diamonds show the respective mean growth rates.

### 6.3.2 Validation – spatial distribution of fish

The distribution of foragers as predicted by the calibrated model showed a much greater match with observed distributions of fish collected during fieldwork than the non-calibrated model. Whilst the original model was able to predict the correct distribution of salmonids within the model (i.e. observed stretches of lower and higher densities were correctly predicted), the degree of accuracy was not as high as the calibrated model with statistical evaluation showed that many were significantly different. Out of a maximum of eight tests of ‘perfect’ (i.e. a 1:1 relationship between predicted and observed densities with intercept of 0,0), the original model could only produce one point that was non-significantly different. The calibrated model was able to increase this number with six elements showing a non-significant difference from perfect prediction with observed patterns, indicating a much better predictive power of salmonid distribution (Table 6.1 and Figure 6.2).

Table 6.1 The ability of the two models to predict observed patterns of distributions of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*), *P* values of the difference between the linear relationship between predicted and observed patterns with that of relationship of perfect prediction (intercept of (0,0) and a slope of one) are shown with numbers in bold indicate a non-significantly different relationship and degrees of freedom in brackets.

Forager class	Original model		Calibrated model	
	Intercept	Slope	Intercept	Slope
Salmon YoY	0.007 (10)	0.001 (10)	<b>0.291 (9)</b>	<b>0.186 (9)</b>
Salmon 1+	<b>0.127 (5)</b>	0.013 (5)	<b>0.989 (5)</b>	<b>0.167 (5)</b>
Trout YoY	0.005 (7)	0.000 (7)	<b>0.170 (7)</b>	0.020 (7)
Trout 1+	0.003 (10)	0.000 (10)	<b>0.111 (10)</b>	0.027 (10)

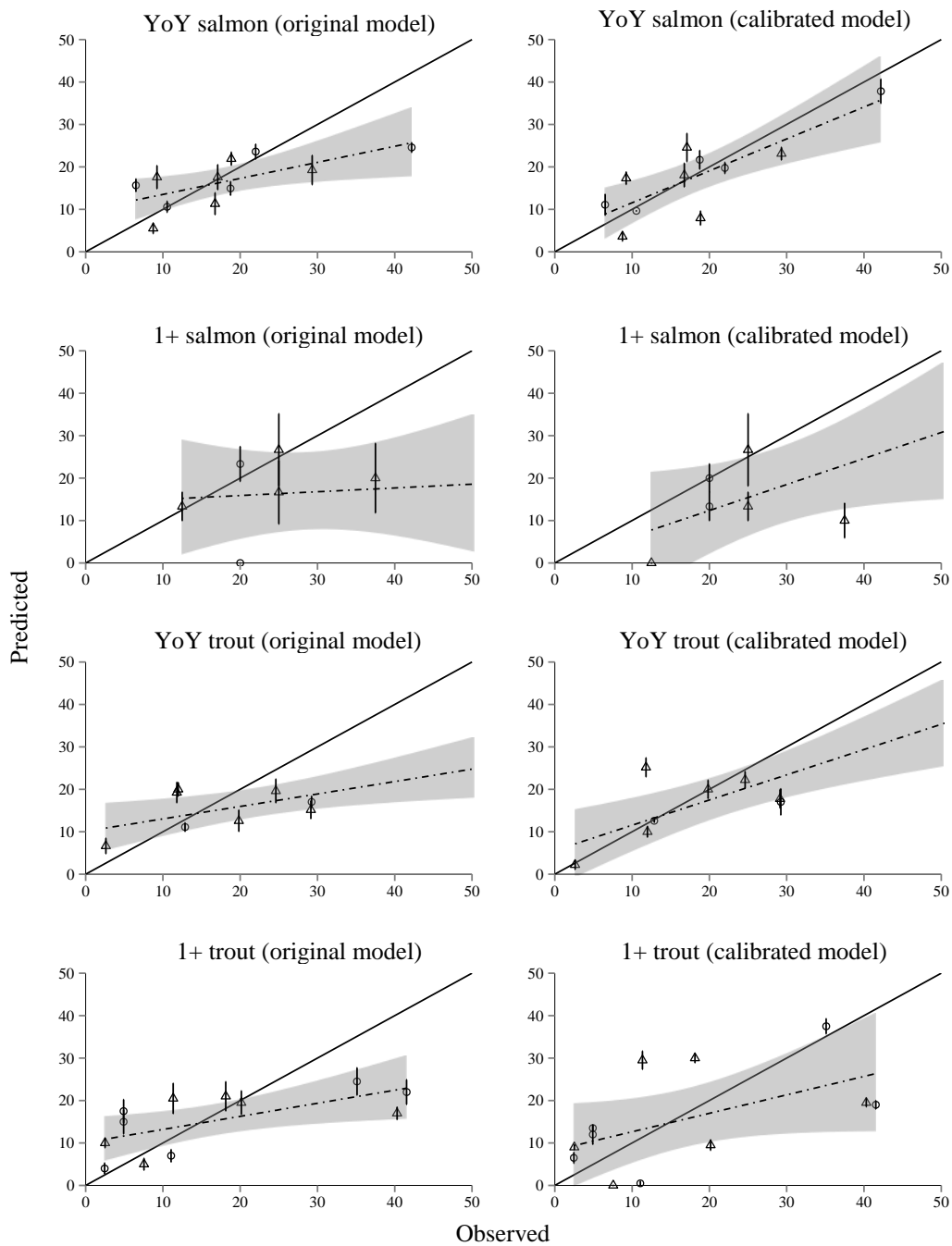


Figure 6.2 The ability of the uncalibrated (original) and calibrated model to accurately predict the distribution of fish under conditions of aquatic macrophyte removal; predicted distributions are plotted against observed distributions. A linear regression model of the relationship is represented by the dotted line whilst the solid line represents a 1:1 ratio (perfect prediction). The shaded area shows the 95% confidence intervals for the regression line. The forager types are young-of-year (YoY) Atlantic salmon (*Salmo salar*), YoY brown trout (*Salmo trutta*) and year old (1+) brown trout (top, middle, bottom graphs respectively). The time steps are corresponding to the same timesteps of sampling events (electric fishing) performed on the observed fish population at the study site.

### 6.3.3 Predicted impact of macrophyte management

Growth rates of all forager classes are predicted to decrease in conditions of reduced *Ranunculus spp.* cover (Figure 6.3). YoY salmonids display a greater sensitivity to the reduction with greater decreases in predicted growth rates than 1+ conspecifics. YoY Atlantic salmon show the greatest difference between with and without *Ranunculus spp.* treatments with a disparity of 0.6% bodymass.day<sup>-1</sup> in mean growth rates in the Sep-Oct period.

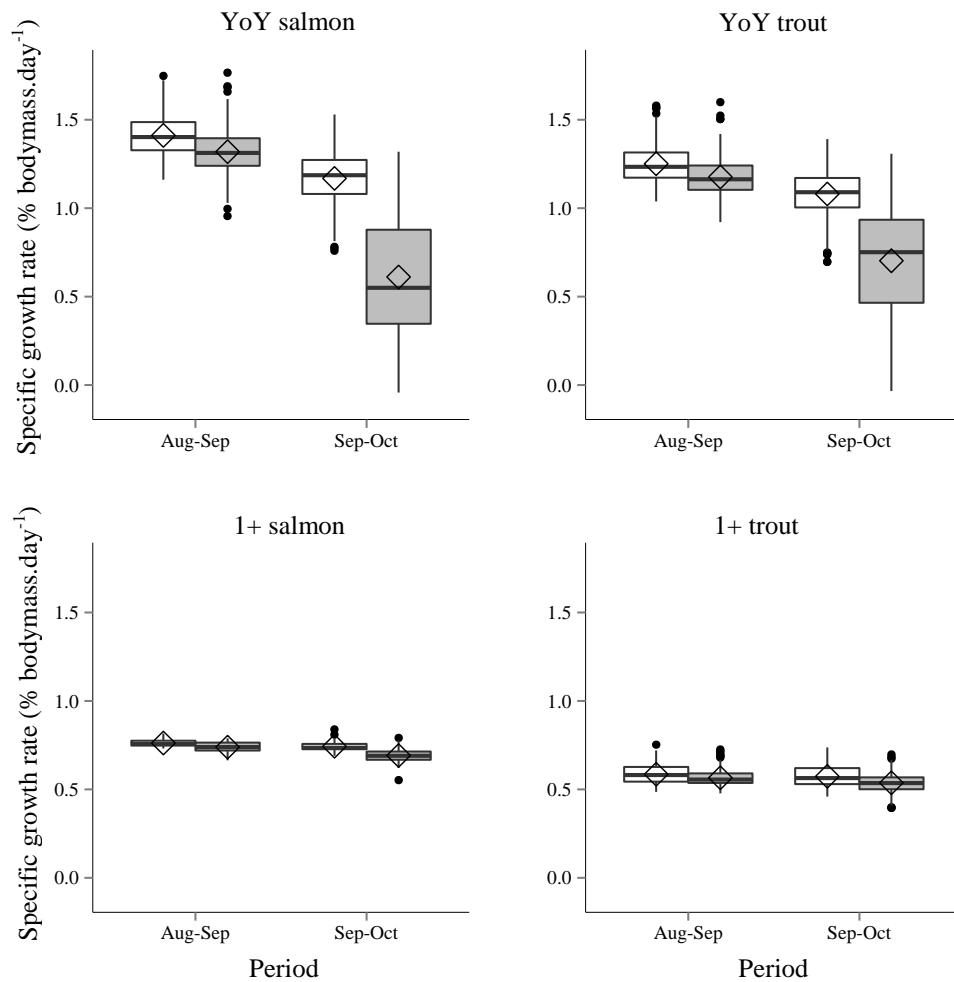


Figure 6.3 The predicted growth rates by the calibrated model of young-of-year (YoY) and one year old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) under natural *Ranunculus spp.* cover (white) and removed *Ranunculus spp.* cover (grey).



## 6.4 Discussion

The loss of overhead cover associated with the removal of *Ranunculus spp.* is predicted to have a negative effect on the growth of YoY salmonids more than their 1+ conspecifics. The original model initially overestimated the salmonid growth rates but was improved through the introduction and calibration of salmonid adaptive behaviour in response to stress to the lack of overhead cover. This improved the ability of the model to predict the spatial distribution of fish in the system. The relative sensitivity of Atlantic salmon and brown trout to overhead cover, interpreted from the calibrated stress parameters that  $S_{\text{Atlantic salmon}} > S_{\text{brown trout}}$ , are in congruence with empirical studies of fish behaviour and this is an unplanned but welcome additional support for model validation (Pickering et al. 1987; Grimm & Railsback 2005). Scenario testing of the new calibrated model under two scenarios of weed management indicates that the increased stress brought about by the removal of overhead cover provided by *Ranunculus spp.* depresses salmonid growth rates. These findings suggest that the cover provided by *Ranunculus spp.* is important for salmonid growth and if removal is necessary, not all of the stand should be removed so that some cover remains.

Reference points of salmonid growth rates and distribution under a regime of *Ranunculus spp.* removal were collected from fieldwork studies. Impacts on local resource density (invertebrate drift) and river hydrology (depth and velocity) were either respectively measured or estimated. In chapter 3, the original model demonstrated its ability to predict population patterns in response to flow and resource density characteristics but it overestimated the growth rates of both Atlantic salmon and brown trout when the virtual environment was parameterised to reflect the conditions of *Ranunculus spp.* removal. Thus it indicates that the original model overlooked a process that potentially limits its predictive power in environments with little or no aquatic macrophyte cover.

Pickering et al. (1987) observed increased concentrations of blood cortisol ('stress hormone') in salmonids in a treatment without access to overhead cover and that concentrations were much lower when overhead cover was provided. Stress can negatively impact the bioenergetics of a fish (Gregory & Wood 1999) and this is where the stress impact affected foragers in the model. The calibration of the species-specific stress parameter suggests that of the two salmonids, Atlantic salmon were more sensitive to the loss of overhead cover than brown trout as  $S_{\text{Atlantic salmon}} > S_{\text{brown trout}}$ ; a result that agrees with the empirical, tank-based investigation by Pickering et al. (1987). Pickering et al. (1987) suggests that their findings were caused by species differences in behavioural response to light or the position of the fish in the water column during feeding. Ultimately, they argued that overhead cover provides the necessary conditions for optimal forging of Atlantic salmon and that without this cover growth rates would be impacted. The utilisation of overhead cover is potentially an adaptive antipredator behaviour in response to avian predation (Allouche & Caudin 2001). At the Mill Stream, avian predators of salmonids are typically grey heron (*Ardea cinerea*) and common kingfishers (*Alcedo atthis*) (personal observation) and could be a contributing factor in observed growth rates. Notably, this investigation started with the 'end-result' (lowered growth rates) and progressed to the individual, finding similar results as Pickering et al. (1987) and this is a successful example of 'inverse-modelling' (Grimm & Railsback 2005).

One of the strengths of the original model (see Chapter 3) was that despite a deliberate decision not to calibrate any parameters, it was still able to produce similar results across several patterns and was validated under a pattern-orientated modelling approach proposed by Railsback and Grimm (2005). The calibration of stress parameter in this investigation means that the model is 'tuned' to create observed patterns. This was taken into consideration and calibration was performed on fish growth rates but validation was performed on a separate, independent pattern of fish

distribution. The noticeable improvement in the ability of the calibrated model to predict the spatial distribution of all fish groups shows that the calibrated model has improved in its representation of salmonid behaviour.

However, model results contradict Roussel et al. (1998) who found a higher distribution of Atlantic salmon in habitats without *Ranunculus spp.* Further confusion is created as some studies show that overhead cover attracts higher densities of brown trout (Butler & Hawthorn 1968) and Atlantic salmon (Kalleberg 1958). Methodological differences between the studies may explain the contradictory findings; Roussel et al. (1998) observed their fish in a natural river system whilst Butler & Hawthorn (1968) and Kalleberg (1958) performed their studies using artificial stream setups. Roussel et al. (1998) measured population density by electric fishing, however lack of a physical structure (e.g. stop nets; they used a buffer strip) to separate sites with and without *Ranunculus spp.*, would fail to prevent the movement of Atlantic salmon from either between or out of fished sites. This highlights the difficulty of sampling and experimental studies in large river systems (Cowx et al. 2001; Penczak et al. 1998). A major benefit of a pattern-validated IBM approach is that it allows for complete observation of foragers and overcomes biases in sampling.

Management must consider several important parameters when designing a regime of *Ranunculus spp.* removal including but not limited to i) the timing of the regime, ii) how much to remove and iii) alternative, non-removal regimes of *Ranunculus spp.* control (Dawson 1989). If *Ranunculus spp.* stands are managed early in the growing season, it can lead to greater synchronised growth that may lead to a stand biomass similar to if removal did not occur at such an early stage; as growth rates increase as the removal improves conditions for growth (Dawson 1979a). The increase to flood risk created by *Ranunculus spp.* stands may even decline if left unmanaged as *Ranunculus spp.* stands go through a ‘four-year-effect’ whereby biomass falls to half that of a routinely managed site (Dawson 1979a). When

necessary, *Ranunculus spp.* management should adopt ‘pre-emptive’ cutting where stands are managed in autumn to reduce the standing biomass at the start of the next growing season (Dawson 1989) but there may be required habitat conditions for this to be effective (Westlake & Dawson 1986). The salmonid IBM model could be used to predict the effect the timing of macrophyte removal on salmonids to identify if there is a timing period that would fulfil both the mitigation of flood risk whilst minimising total impact on salmonid growth rates. The use of natural or artificial shading from either bankside riparian growth or the dragging of an opaque shade over the river are two examples of alternative methods to reducing *Ranunculus spp.* biomass (Dawson 1989, Dawson & Hallows 1983). These may be more salmonid-sympathetic macrophyte removal regimes as they do not remove all of the stand growth. If cutting is necessary, the selective removal of certain stands based on their location within the channel may produce a situation which sufficiently reduces flood risk whilst maintaining the necessary habitat required for salmonid growth. The impacts on salmonid growth could be predicted through the use of a model like the one developed in this investigation.

In summary, this investigation highlights the importance of *Ranunculus spp.* stands for a healthy salmonid population. In addition to its physical impact on channel flow, *Ranunculus spp.* also impacts salmonid populations by providing overhead cover and if removed, fish become stressed, resulting in lowered growth rates. Any *Ranunculus spp.* management, either for flood mitigation and improving fishing access, should consider these unwanted impacts during their design phase. The multitude of parameters that must be considered when designing a *Ranunculus spp.* management regime (e.g. timing, extent of cut, etc.) makes it a challenge to devise an effective program. The model developed here is one possible tool that can be used to quantify the impacts alternative *Ranunculus spp.* management regimes have on salmonid growth and a compromise that meets both the aim to mitigate flood risk with minimal impacts on fish populations can be sought.

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## **7. Predicting predator impacts on salmonids in a riverine environment**

### **7.1 Introduction**

Predators play an important role in maintaining the overall population balance within an ecosystem (Thorp 1986; Leibold et al. 2004; Ripple & Beschta 2006; Chapin et al 2000; Estes et al. 2011). The behavioural interactions at the scale of individuals, between predator and prey, exert a significant effect on prey populations (Reynolds & Tapper 1996). In chalk stream fisheries in south England, the culling of the salmonid predator, European pike (*Esox lucius*), to remove predation pressure is a commonly adopted management regime (Mann 1989). Despite the implementation of this radical management of pike populations, there have been few investigations into the overall effect the removal of pike has on brown trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) populations (see Mann 1985; Mann 1989). However, given the intimate and large effect of predator-prey relationships, a better understanding of the extent of predator impact on salmonid populations should be understood prior to the implementation of a potentially destabilising management regime (Myers et al. 2003; Reynolds et al. 1996; Ballard et al. 2001).

European pike are top fish predators in chalk stream environments and have a predominately piscivorous diet, predating on salmonid and non-salmonid species with a recorded preference for the former (Mann 1982; Jepsen 1998). Predator effects on prey are classified as either i) lethal or ii) nonlethal. Nonlethal effects manifest themselves through the adoption of anti-predator behaviours (Lima 1998) with examples including the avoidance of area(s) where predators are found, favouring less conspicuous behaviours in the presence of a predator (e.g. feeding vs. hiding) and/or the selection of habitats that may confer reduced predation risk (e.g. favouring habitat with greater cover) (Greenberg 1999; Dill & Fraser 1984). These



behaviours increase prey survival by minimising the risk of predation but as these behaviours involve diverting time and energy to non-feeding activities time budgets are altered which will affect prey growth rates (Lima 1998).

Proponents against pike culling argue that its preference for non-salmonid prey fish means that the total biomass of salmonids consumed is relatively small and thus the removal of the predator does not achieve significant positive results. Furthermore, Packer et al. (2003) suggests that the majority of salmonids consumed by pike have been weakened through disease and so predation is beneficial as it limits disease spread. Finally the cannibalistic behaviour of pike acts as a self-regulatory population process; removing large pike will remove the primary source of predation of small pike (Mann 1982) with small pike densities increasing as consequence (Mann 1985; Mann 1989). Fish vulnerability to pike predation is determined by maximum gape size of the predator (Nilsson & Bronmark 2000) and more small pike predators is likely to increase the predation risk and number of both lethal and nonlethal interactions experienced by small salmonids.

The multiple and complex predator-prey interactions remains poorly understood (Mann 1989). Lima (1998) argues that the cumulative effect of nonlethal predator-prey interactions may exceed lethal interactions. Field-based predator-prey interactions are inherently difficult to obtain (Craig 2008) but behavioural understanding is highly relevant for population management (Caro 2007). Here we present an individual-based model (IBM) of salmonid and pike in a virtual chalk stream environment to investigate the nonlethal impacts of predator-prey interactions. The modelling approach allows for the integration of antipredator behaviour to model nonlethal interactions. The objective is to provide a quantifiable assessment of the non-lethal impacts of pike on salmonid populations by modelling the energetic cost of antipredator behaviour on salmonid growth as a step towards evidence-based management.

## 7.2 Methodology

### 7.2.1 Overview

A previously validated salmonid IBM is modified to model the dynamic movement and interactions between European pike (*Esox lucius*) and brown trout (*Salmo trutta*) (see chapter 3 and chapter 6 for detailed model description). Observed interactions between pike and salmonids from a fieldwork study is used as a reference to model interactions between virtual foragers.

### 7.2.1 Fieldwork – (July – October 2011)

#### 7.2.1.1 Construction of two study sites

Trout behaviour and growth rates in response to predation pressure were collected over a 12-week period beginning in July 2011. Two stretches of river, ‘Stretch A’ (upstream) and ‘Stretch B’ (downstream), both within the Mill Stream (see chapter 2), were delineated through the construction of fish barriers (25mm x 25mm galvanised 14 gauge wire mesh). The fish barriers spanned the width of the channel with its vertical construction involving a section of wire mesh (30cm) flush with the riverbed upstream of the barrier and the top finishing 30 cm above mean water. The fish barrier was secured with fence poles driven into the riverbed and any gaps between riverbank and barrier were blocked with rubble bags filled with riverbed substrate. The barriers were cleaned of any debris/leaves daily to maintain normal flow rates in and out of the delineated stretches. The size of the gaps in the wire mesh prevented movement of fish with body depth >25mm in or out of the stretch (i.e. salmonids of ages greater than 1+).

#### *7.2.1.2 Salmonid densities per stretch*

During electric fishing surveys, each stretch was split into two smaller sections by stop nets and a two-pass depletion electric fishing methodology was used to sample fish populations. Regulated fish handling procedures were performed under Home Office project license project license 'Ecology of Freshwater fish' PPL 30/2626. See chapter 2 for detailed description of fish handling and PIT tagging procedure. A total of 89 brown trout with FL > 130mm had a 23 x 3.6 mm and 32 brown trout with FL < 130mm had a 12.0 x 2.12 mm, half-duplex passive integrated transponder (PIT) tag (ISO 11784/11785, OregonRFID,) inserted into their peritoneal cavity to allow for individual identification and tracking. All Atlantic salmon caught had hatched the same year (young-of-year, YoY) whilst brown trout showed a more varied age assemblage.

To increase the observable signal of the response by the salmonid population to predators, the density of salmonids within each stretch were increased through the addition of 1+ brown trout caught from two areas; 1) areas of the Mill Stream not within the sectioned areas and 2) the Tadnall Brook, a tributary of the River Frome. Following the same fish handling procedure, all fish were similarly tagged for identification using 23.6mm HDX pit tags. These fish were released into the two stretches and increased the density of 1+ trout to densities similar to that experienced in fisheries that undergo a regime of stocking. Furthermore, an increase in density would also intensify the impacts of predation pressure on salmonid populations and would increase the likelihood of detecting an effect at the population level. The number of 1+ trout added to stretch A and stretch B to raised density from 0.019 ind./m<sup>2</sup> and 0.020 ind./m<sup>2</sup> and 0.045 ind./m<sup>2</sup> and 0.042 ind./m<sup>2</sup> respectively.

### *7.2.1.3 Treatment regime*

The fieldwork period was divided into two six-week periods called: period 1 and period 2. The first period (period 1) was the ‘control’ period where the salmonids in both stretch A and stretch B were not subject to any pike predation (i.e. no pike were present within either stretch). After six weeks, both stretches were electric fished to recapture tagged individuals. After this period, the ‘treatment’ period (period 2) began and 3 days after being electric fished (to allow for fish recovery), three pike (mean FL = 450mm) were introduced into stretch B whilst stretch A remained pike-free. The treatment stretch (stretch B) was located downstream of the other stretch to remove the probability of water-borne chemical cues, either prey or predator produced, that would illicit anti-predator behaviour (Chivers & Smith 1998) affecting the other stretch. The treatment period also lasted a total of six weeks and both stretches were electric fished again to measure the bodymass of tagged fish.

### *Calculating salmonid growth*

The growth rates of recaptured, tagged salmonids of each stretch for each period are calculated in terms of specific growth rates or the percentage change in body mass per day (% day<sup>-1</sup>). This is expressed as:

$$SGR = \frac{\ln(W_{salmonid\ t_n}) - \ln(W_{salmonid\ t_0})}{t_n - t_0} * 100$$

Where SGR is specific growth rate,  $W_{salmonid\ t_0}$  is the mass at the start of the period ( $t_0$ ) and  $W_{salmonid\ t_n}$  is the mass at the end of the period and  $t_n - t_0$  is the number of days between recapture.

### *Tracking spatial distribution of salmonids*

The location or patch occupancy of tagged fish was recorded by using a portable HDX PIT tag antenna (HDX Backpack Reader, Oregon RFID). See chapter 2 for description of equipment and tracking method.

## 7.2.2 Model description

### 7.2.2.1 Model overview

This model adapts the model created in chapter 6 (i.e. the effect of overhead macrophyte cover on fish growth rates and behaviour is included). The improvements made to the model primarily pertain to the movement from a static (environmental) predator parameter to a more realistic representation of predator (pike) behaviour. This is done through the creation of ‘predator’ forager types that are dynamic and can move within the virtual environment. An improved representation of pike behaviour will lead to a more realistic predator-prey (salmonid-pike) interaction in the model. The same size classification of pike (i.e. small or large pike) was used with a threshold size of 218mm (see chapter 3). Static predation pressure as an environmental parameter is no longer referenced in any equation.

### 7.2.2.2 Virtual environment

The virtual environment is based on the 2008 environmental dataset (see chapter 2). All parameters pertaining to environmental characteristics remain the same with aquatic macrophyte cover as observed under a non-managed, natural scenario.

### 7.2.2.3 Predator forager types

There are a total of 14 new forager (predator) types and these correspond to the size of the predator (small vs. large) and the stretch the predator first enters (stretch 1-7). The number of predators is defined per specific scenario (see the ‘*Scenario of pike densities*’ section later).

### 7.2.2.4 Predator interactions

As a salmonid-centric model, predator growth rates are not modelled and so they do not consume any resources nor expend any energy. They have the ability to move from patch to patch and follow a patch selection rule derived from known and observed pike behaviour. Pike are typical ambush

predators (Cook & Bergersen 1988; Helfman et al. 1997, Knight et al. 2008), preferring habitat that is deep and with slower current speeds (Lamouroux et al. 1999). Predators in the model select patches that are both deep and slow with the two parameters sharing an equal importance and the select the patch with the highest fitness measure defined by:

$$FM_{Pike} = 100 + P_{Dep.} - P_{Vel.}$$

Where FM is the fitness measure,  $P_{Dep.}$  is patch depth &  $P_{Vel.}$  is patch velocity.

Pike have home ranges of varying sizes and whilst there is some overlap of these ranges, they are generally solitary fish (Hodder et al. 2007, Knight et al. 2008). This behaviour is modelled by having patches that are already occupied by a pike return a fitness measure of 0.01 (i.e. pike avoid patches already occupied by other pike). A patch is selected by random if all patches a pike can move into return the same fitness measure. Pike movement is limited to one patch upstream or downstream in distance per timestep (hour).

#### *Predator processing order*

At the start of each timestep, predators are processed before salmonid foragers with big pike moving first. Predators within the same predator type are processed randomly.

#### *Salmonid foragers*

The only alterations to salmonid foragers performed are to the processing order, patch fitness measure and starting populations.

#### *Salmonid forager processing order*

Salmonid foragers are now processed after predators (see *Predator processing order*) but the order in which salmonid foragers are processed remains the same and oldest foragers processed first. The order foragers within the same age are processed is done randomly.

#### 7.2.2.5 *Salmonid forager patch measure*

This study tested two types of anti-predator behaviours of salmonids in response to predator presence: 1) predator avoidance and 2) cessation of feeding whilst in the presence of a predator. The two behavioural responses were tested independently of each other.

##### 1. Predator avoidance

Salmonid antipredator behaviour is the avoidance of patches occupied by pike. From field observations, patches occupied by pike were not completely avoided by trout; rather there was a 76% decrease in the frequency of use of the patch (13) most occupied by pike (see Figure 7.2). There was no difference in the body weight between salmonids that avoided the patch and those that utilised the patch (see Figure 7.3). Thus, in this anti-predator behaviour scenario, patches occupied by pike were avoided by salmonids 76% of the time. No other modifications to other salmonid behaviour were altered.

##### 2. Cessation of feeding

Salmonid antipredator behaviour is the cessation of feeding behaviour. As drift feeders, feeding involves the movement of the salmonid into open water and this exposure represents a higher predation risk than when the salmonid is resting (either in cover or near the substrate). Studies have observed salmonids reducing feeding activity in the presence of predators (Dill & Fraser 1984). In this anti-predator behaviour scenario, if a predator occupies the same patch as a salmonid their maximum consumption rate for that timestep or  $C_{max}$  (see chapter 3) will be reduced to zero and will remain that for as long as there is a predator present.

#### 7.2.2.6 Salmonid starting populations

The starting population density of salmonids reflects the densities during the 2011 fieldwork study but the starting proportional distribution reflected the distribution observed in 2008. The total density of 1+ trout individuals across the entire virtual environment was increased from 0.008ind.m<sup>2</sup> as recorded in 2008 to 0.042 ind.m<sup>2</sup>. The distribution of the starting locations for 1+ foragers (i.e. the stretch that a Trout 1+ entered at the start of a model simulation) was not altered (see Table 7.1).

Table 7.1 Densities and distribution of 1+ brown trout (*Salmo turtta*) foragers in this model simulation compared to the pattern recorded in 2008. The densities were increased to reflect the densities of 1+ trout in fieldwork experiments into European pike (*Esox lucius*) and salmonid interactions. Numbers in brackets indicate the density of trout in ind.m<sup>-2</sup>.

Stretch	Number of 1 + trout foragers	
	2008	This investigation
1	8 (0.024)	40 (0.122)
2	5 (0.011)	25 (0.056)
3	7 (0.015)	35 (0.077)
4	4 (0.009)	20 (0.044)
5	0 (0.000)	0 (0.000)
6	0 (0.000)	0 (0.000)
7	1 (0.002)	5 (0.008)
Total	25 (0.008)	125 (0.042)

#### Number of model replicates

Following the analysis in chapter 3, the number of replicates per scenario was set at five.



### *Scenarios of pike densities*

This investigation tested the impacts pike predators have on salmonid growth rates under four different plausible pike densities. The two antipredator behaviours being investigated are tested at all four pike densities. The four densities are:-

1. Observed pike densities

The number of pike present in reflected the densities and distribution of pike as observed in the Mill Stream under natural conditions (no pike nor weed management) as in 2008 (see chapter 2).

2. No pike

There are no pike predators present in the model to represent a total and effective predator culling management regime.

3. High densities of large pike

The number of large pike is at densities as recorded during fieldwork experiments into pike-salmonid interactions collected in 2011. This is four times the density of large pike as observed in natural conditions in 2008. No small pike are present to illustrate the impact of cannibalism by large pike (Mann 1982).

4. High densities of small pike

There are no large pike present but there are high densities of small pike; this reflects a management regime that is efficient at removing large pike and as a result of their removal, with no cannibalism, small pike densities are higher (Mann 1985). The increase in small pike densities is equivalent to the increase in large number of pike as in the previous scenario at four times the observed densities of small pike under natural conditions.

## 7.3 Results

### 7.3.1 Fieldwork

#### *Observed predator impacts on salmonid populations – growth rates*

In the absence of pike, mean growth rates of tagged trout 1+ during the field study in stretch A and stretch B did not significantly differ (t-test,  $p>0.05$ ) (Figure 7.1). However, when pike were added to stretch B, growth rates of trout 1+ with pike were significantly lower than trout 1+ in stretch A, which had no pike (t-test,  $p<0.01$ ). There was no difference in growth rates of trout 1+ in stretch A between the two periods (t-test,  $p<0.01$ ).

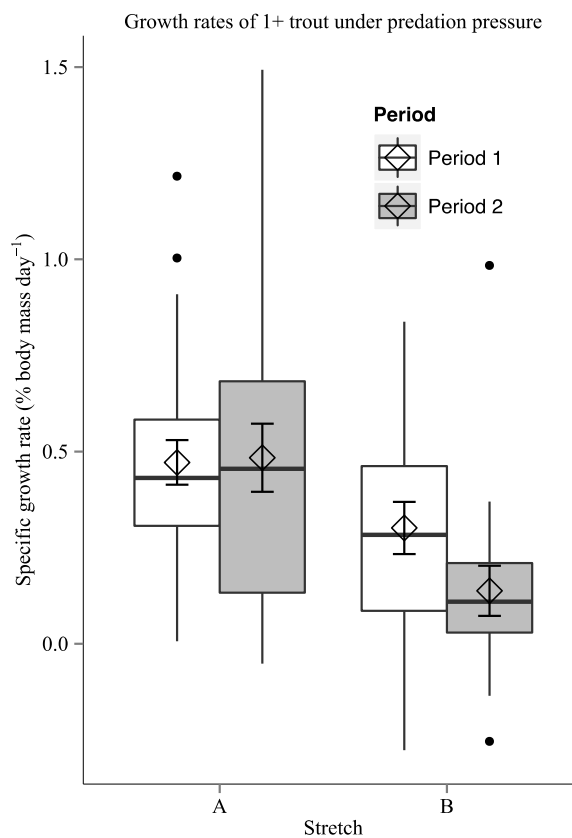


Figure 7.1 The observed growth rates of one-year-old (1+) brown trout (*Salmo trutta*) under different predation pressures from field data collected in 2011. Mean growth rates are shown by the diamond symbol with error bars indicating standard error. Fish were counted in two stretches (A and B) by fish barriers and in period 1 no European pike (*Esox lucius*) were present in either stretch. During period 2, no pike were added to stretch A and pike ( $n=3$ , mean fork length = 412mm) were added to stretch B. Growth rates between the two stretches were not significantly different in period 1 (t-test,  $p>0.05$ ) but were significantly less in stretch B in period 2 (t-test,  $p<0.01$ ).

*Observed predator impacts on salmonid populations – distribution*

Tracked locations of tagged 1+ trout in stretch A and stretch B showed an uneven distribution, with a high preference of a few patches (Figure 7.2). Some patches accounted for nearly 40% of all locations of tracked individuals whilst there were several patches where no trout 1+ were tracked. There was a slight variation in patch use in stretch A between period 1 and 2 (pike absent during both periods). In stretch B, during period 2 (when pike were introduced), there was a 76% drop in the use of patch 13 compared to period 1 (no pike). Patch 13 is the patch that was occupied most by pike when they were introduced in stretch B, with 44% of total pike trackings. Although there was an overall decrease in the use of this patch by trout, some trout still were tracked using this patch.

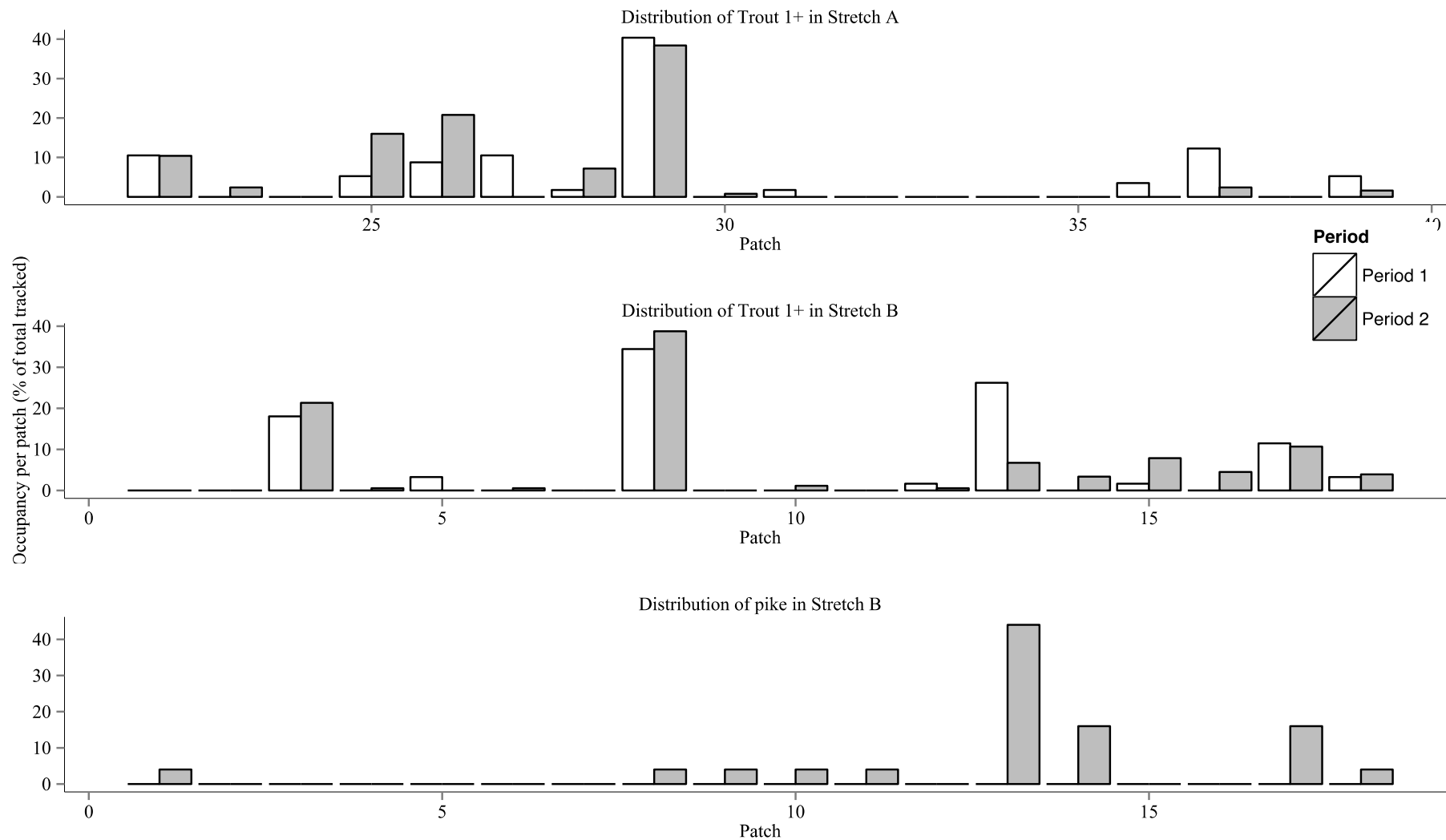


Figure 7.2 The distribution of one-year-old (1+) brown trout (*Salmo trutta*) and European pike (*Esox lucius*) in two stretches enclosed by fish barriers. Pike (n=3, mean fork length = 452mm) were added to stretch B in period 2 but no pike were added to stretch A.

*Size difference between Trout 1+ individuals in patches with and without pike*

There was no significant size difference between the tagged 1+ trout that were tracked using the patch most occupied by pike (patch 13) with those that avoided the patch (t-test,  $p>0.05$ ) (Figure 7.3).

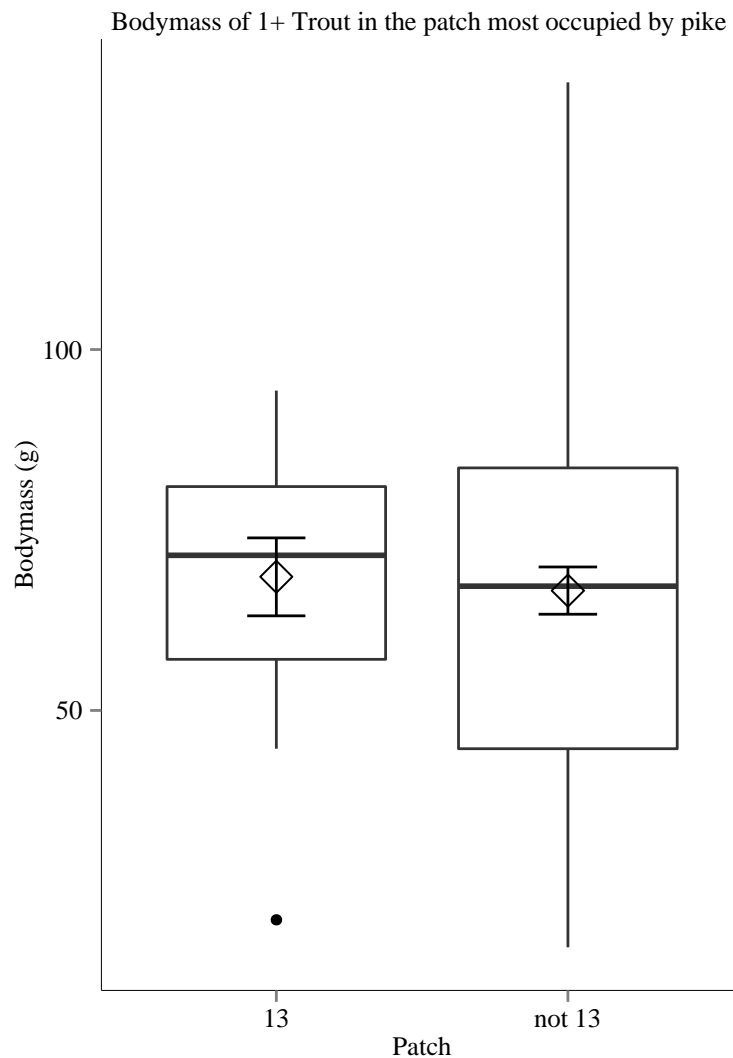


Figure 7.3 The body mass of 1+ (age) brown trout (*Salmo trutta*) that were tracked occupying patch 13, the patch most preferred by pike (*Esox lucius*) in a stretch where emigration from the stretch was prevented by the use of fish barriers. Mean body mass are displayed by the diamond symbol with standard error bars; there was no significant differences between the two (t-test,  $p>0.05$ ).

### 7.3.2 Modelling results

#### *Salmonid anti-predator response - avoidance*

The growth rates of the three salmonid forager types (Trout 1+, YoY trout and YoY salmon) did not differ under the different predator densities modelled (Figure 7.4). The presence of pike in the model had very little impact on predicted forager growth rates. Some YoY trout and YoY salmon did however experience negative growth with the latter predicted to show more extreme loss than the former.

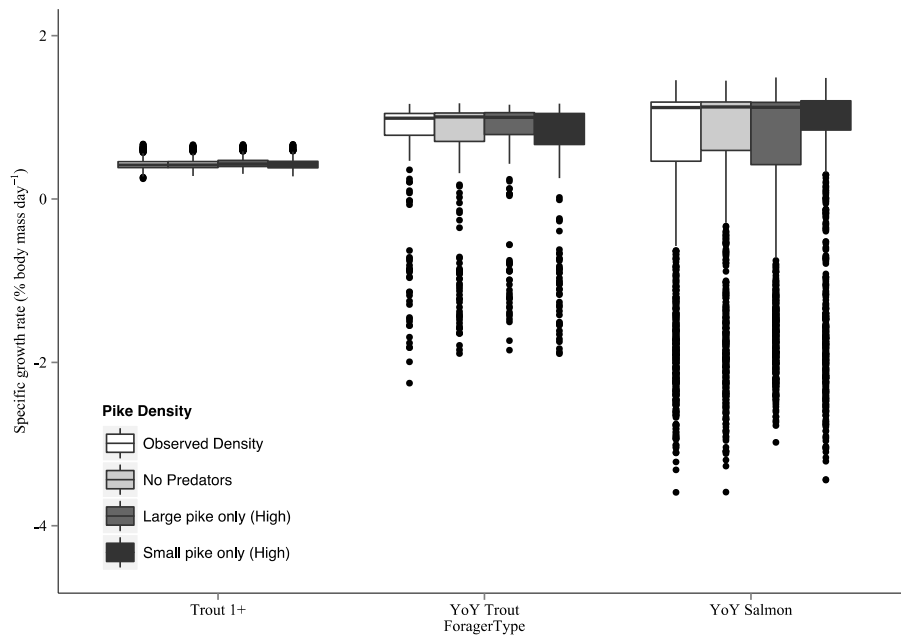


Figure 7.4 Predicted growth rates of three salmonid classes, young-of-year (YoY) and one-year-old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in response to different predator densities in the model. 1+ trout are only vulnerable to large pike (fork length > 218mm) whilst YoY salmonids are vulnerable to both large and small pike (FL < 218mm). The salmonids respond to predators by avoiding the patch that the predators are located and consequently, select the patch (of the remaining patches) with the highest consumption rate. The scenarios of high large and small pike densities are four times higher than observed densities of each respective pike size.

### *Salmonid anti-predator response - feeding cessation*

The growth rates of all three salmonid forager types (1+ trout, YoY trout and YoY salmon) showed a negative response to increasing predator densities but the sensitivity in response was a lot greater in the younger age classes (Figure 7.5). Additionally, all three forager types displayed the lowest growth rates under the greatest density of predators they were vulnerable to.

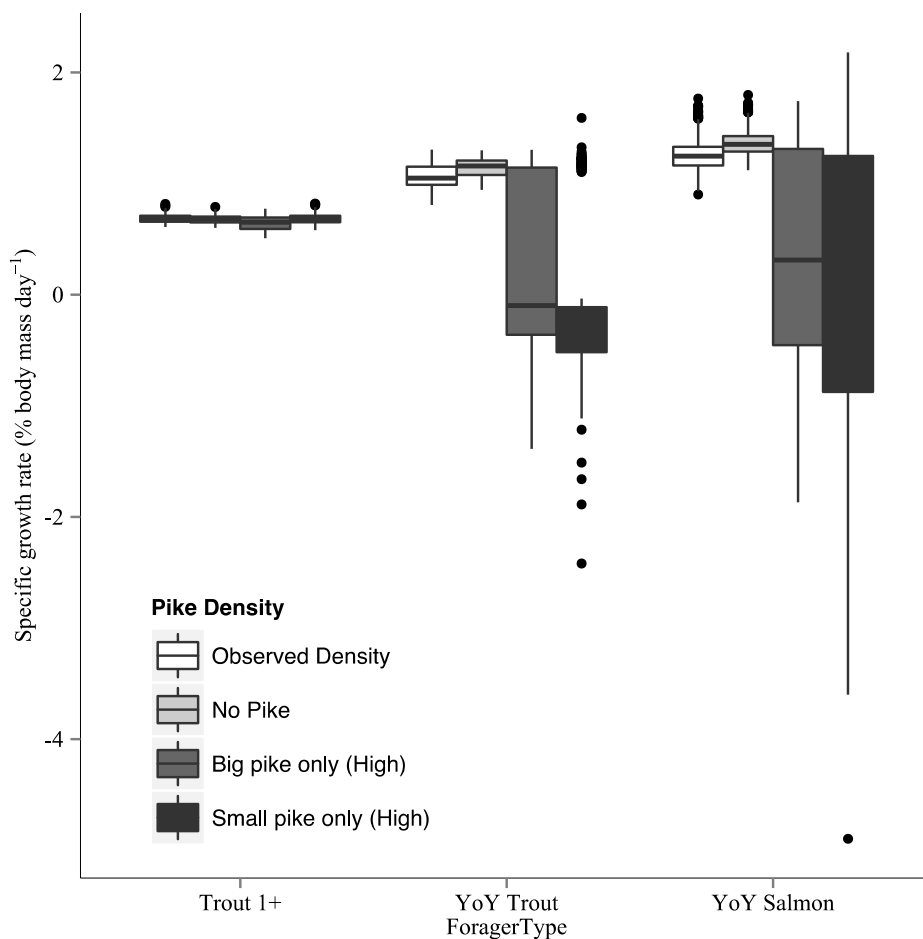


Figure 7.5 Predicted growth rates of three salmonid classes, young-of-year (YoY) and one-year-old (1+) Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in response to different pike (*Esox lucius*) densities in the model. Trout 1+ are only vulnerable to large pike (fork length > 218mm) whilst YoY salmonids are vulnerable to both big and small pike (FL < 218mm). The salmonids respond to predators within the same patch by ceasing feeding behaviour. The scenarios of high large and small pike densities are four times higher than observed densities of each respective pike size.

## 7.4 Discussion

The empirical data collected in this investigation indicates that 1+ trout grow faster in the absence of pike as the growth rates of 1+ trout are negatively affected by the presence of pike (Figure 7.1). This result matches the study into predator impacts on salmonid behaviour by Biro et al. (2004). Modelling the effects two different antipredator behavioural responses predicts the decrease of growth rates only occurs in the antipredator behaviour of feeding cessation. No decrease in growth rates was predicted with the antipredator behaviour of avoiding patches occupied by predators. However the fieldwork study recorded salmonids avoiding patches occupied by pike (76% of the time) and this contradiction between observed and predicted growth rates with this antipredator behaviour suggests that salmonids may adopt a mixture of these two antipredator behaviours. The cessation of feeding was not measured during fieldwork but modelling this behaviour and the predicted resulting decrease in salmonid growth rates, suggests that this behaviour may be adopted by real salmonids in chalk streams. IBMs can add to theoretical understanding of the links between predator-prey relationship at individual and population level (Grimm & Railsback 2005).

The two types of antipredator behaviours investigated have been observed in behavioural studies of predator prey interactions in fish and mammals (Gregory 1993; Lima 1998). Separating and making the two antipredator behaviours independent of each other in model simulations produced interesting results when interpreted within an evolutionary context and salmonid survival. Avoiding the areas of habitats where predator are present decreases the chance of a potentially lethal (for prey) interaction with a predator and this was empirically observed during the fieldwork study. However, when virtual salmonids are modelled with this antipredator behaviour, the mismatch between predicted and observed growth rates needs to be addressed.



Prey growth rates are not always negatively affected in the presence of predators (Morin 1986) and the lack of an affect on growth rates predicted by the model is thus not entirely unrealistic. Fish will alter their habitat use in the presence of predators (Gregory 1993) and this was observed during fieldwork as 1+ trout avoided patches most commonly occupied by pike. Predator avoidance behaviour can lead to a decrease in salmonid growth rates because as salmonids avoid certain patches, the densities in the remaining patches would increase resulting in greater density dependence processes; increased densities negatively affecting growth rates have been demonstrated in chapter 4. However, simulations where the density of 1+ trout and pike matched the densities during fieldwork (Figure 7.4 and Figure 7.5 ‘observed density’) suggest one possible reason to explain the lack of a predicted effect on growth rates is that the area avoided is too small. If the modelled area avoided is smaller than reality, the effect of this avoidance behaviour is underestimated in model simulations; avoidance distances larger than one patch would exacerbate distribution effect leading to increased densities in the remaining patches. The intensity of fish antipredator behaviours varies between individual fish (Dannevit & Petersson 2001). Fieldwork observations of trout 1+ patch use in the presence of pike indicate the distribution of avoidance distances is not constant and spanned from no avoidance to avoiding at a distance of three patches. Predator cues utilised by prey include visual confirmation, the release of pheromones and/or other protein cues either from the predator itself or injured prey (Chivers & Smith 1998; Elvidge et al. 2013). Variation in the intensity of antipredator response (i.e. the variation in the avoided distance as seen in fieldwork) may be due to intra-specific differences in life history, genetics and past interactions with predators (Brown et al. 2006; Vilhunen & Hirvonen 2003; Jackson & Brown 2011). Further complexity exists as environmental conditions affect the type and intensity and type of antipredator behaviour adopted by salmonids (Gregory 1993; Allouche & Gaudin 2001).

The discrepancy between predicted and observed growth rates from simulations of predator avoidance is an indication that antipredator behaviour in salmonids is complex and consists of more than just predator avoidance. Simulations of an alternative antipredator behaviour, that of cessation of feeding if a pike is present in the patch, predicted a fall in growth rates and this matches empirical field data. The cessation of feeding behaviour was not recorded in salmonids during field experiments; the continuous observations required to measure such an intimate behaviour poses a significant challenge to performing it in the field (Johnson & Li 2010; Copp et al. 1998). As fieldwork methodology did not attempt to measure it, the antipredator response of feeding cessation cannot be ruled out as having occurred by salmonids. Predator presence has been observed to depress salmonid feeding rates (Dill & Fraser 1984) and future simulations should represent a mixture of avoidance and feeding cessation. Other predator-induced effects like stress (Archard et al. 2012) and nocturnal feeding (Railsback et al. 2005) are also possible candidates for inclusion. Future model simulations to investigate this effect may add to our understanding of the link between predator avoidance and growth rates and a potential method that could be used for this complex parameter estimation is Approximate Bayesian Computation (Beaumont et al. 2002).

A temporal scale to describe the trade-off between risk of death from predators and the risk of death from limited growth rates (starvation) may also provide greater realism. Foragers should be able to assess their future fitness when a forager balances the costs of non-feeding (starvation) against predation risk. If the threat of starvation increases due to increased antipredator behaviours, fish may place greater priority on feeding despite the presence of predators (Railsback et al. 2005).

The movement behaviour of virtual pike may also require future refinement as it currently excludes any reference to prey distribution and densities. In this model, predators move and select patches on two habitat characteristics:

patch depth and velocity. Pike have been observed to prefer these patches for the cover they provide and for their low bioenergetic requirements and as typically short-burst, high-energy predators and these patches represent prime habitat. (Helfma 1997; Lamouroux 1999). However, pike movement can have greater diel movements than currently modelled (Hodder et al. 2007). Furthermore, this patch selection measure means that pike do not consider the density of the prey species when deciding which patch to occupy; as it stands currently, the relationship between pike and salmonids is very prey-centric with a focus on the antipredator behaviour of prey. A greater emphasis on predator behaviour towards prey distribution and behaviours should prove positive in predicting predator-prey relationships (Lima 2002). However, this challenges the MORPH modelling platform and MORPH was initially written for the construction of bird IBMs and trophic hierarchy between foragers is not currently supported (Stillman 2008). Though there may be possible workarounds, the adaptation to the model to include this level of predator-prey relationship may prove impractical and it may be more worthwhile to use an alternative coding platform to construct a new IBM (e.g. *NetLogo*, see Railsback & Grimm 2012).

Considering the caveats of predator-prey complexities described earlier in the discussion, model predicted growth rates under different densities of predator could still be used in evidence-based management of pike culling. The most prominent interpretation of the results is the small difference between predicted salmonid growth rates under a scenario of no predator density and under a scenario of observed predator densities (2008 environmental dataset where there was no management). The observed predator densities was the density of pike under a management of no pike removal and therefore the removal of pike is predicted to have only a small positive effect on salmonid growth rates. As a regime of pike culling has been associated with increased densities of small pike as rates of cannibalism is reduced as larker pike are removed (Mann 1989), simulations of increased small pike densities (with salmonid antipredator behaviour of

feeding cessation in the presence of pike) predict a large effect on young-of-year (YoY) salmonids (Figure 7.5). Unfortunately, field work data on YoY salmonid growth under predation pressure cannot be used to validate this predicted pattern as the number of recaptured YoY salmonids was too low (n=2) and the size of mesh used in the construction of the fish barriers did not preclude the movement of YoY salmonids in and out of the stretch. Further investigation to address the validity of the predicted negative impact in YoY salmonid growth rates under increased densities of small pike is needed to justify a regime of predator culling.

Predator management needs to include the understanding of complex predator-prey relationships when making informed decisions but is a contentious issue due to varied social acceptance of predator culling (see Ballard et al. 2001). Fieldwork data collected in this investigation suggests trout growth rates may be negatively impacted by the presence of a predator. The difficulty in defining predator-prey impacts is a result of the complexity of behavioural options displayed by both parties in predator-prey interactions (Brown et al. 2006). The most important factor driving the implementation of predator culling are the aims of the management; if it is to solely increase the game fishing of a site then there are limited objections to a regime of predator removal (Jolley et al. 2008, Mann 1985). However, given the important role predators perform in maintaining the overall health of the ecosystem (Chapin et al. 2000, Ripple & Beschta 2006), the case for predator culling is weakened if a more holistic approach to fishery management is adopted. Researchers and management should work together to quantify nonlethal effects of pike on salmonid populations, as these potentially are as impactful as lethal effects (Lima 1998; Cresswell 2008). IBMs are a tool that can potentially handle the complexity in predator-prey relationships lending itself to be a suitable option to evaluate predator management regimes.

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## **8. Thesis discussion**

### **8.1 Contribution to salmonid conservation and fishery management**

#### *8.1.1 Thesis overview*

Freshwater habitats are a particularly challenging system to manage, as numerous interested stakeholder groups will have, sometimes very different and at other times very subtle, interests and conflicts. These conflicts can be resolved with a better understanding of the complex relationships between abiotic and biotic freshwater processes as a move to evidence-based, holistic management. In this thesis I have shown how salmonid fishery management in chalk streams faces conflict with flood risk (chapter 6) and conservation managers (chapter 7) and the potential threats from parasites (chapter 5) and the need to identify the limiting processes potentially compromising the success of a management regime (chapter 4); all through the use of a validated salmonid IBM (chapter 3). The challenge for fishery managers is to make decisions with regimes for which there may be a lack of general consensus within the scientific community (Ludwig et al. 1993) and waiting for an agreed decision is potentially a poor option as inaction may result in a worsening scenario. Furthermore, there is growing pressure for the goals of fishery management to move away from specific, angler-targeted trophy fish species and to appreciate the holistic freshwater ecosystem in their management (FAO 2012). In this discussion I interpret chapter specific results within the framework of freshwater management on the River Frome and with suggestions on the future direction of its management.

#### *8.1.2 Recreational fishing impact on the River Frome*

The general assumption is that the primary objective of fishers is to catch trophy fish (Birkeland & Dayton 2005; Arlinghaus et al. 2009) and studies have shown the potential of recreational fishing as a contributor to the global decline in fish populations (Cooke & Cowx 2004). Salmonid fishing

management attempts to limit potential effects through the implementation of regulations including the need for fishing licenses, closed fishing seasons, Net Limitation Orders (NLO) (i.e. catch-limits) and voluntary catch-release schemes (CEFAS & EA 2013) that limit the amount of fishing effort and catch exerted on salmonid populations. However the potential for recreational salmonid fishing on the River Frome as a contributory cause to the observed decline in adult Atlantic salmon populations cannot be ruled out; in 2012, 29% of declared, rod-caught (540) Atlantic salmon in rivers in southwest England were not released, below the 99% of released catch in south England (CEFAS & EA 2013). Though adult salmon are being taken from the River Frome, the management assess the salmon stock health by the amount of eggs deposited by spawning adults as a percentage of a target density, and the number of adult salmon to achieve this is called the minimum spawning stock. In 2012, the River Frome is assessed to have  $1.4 \times 10^6$  eggs deposited which reaches 93% of the conservation limit set at  $1.5 \times 10^6$ , and whilst a little below target, the number of eggs deposited has only fallen below this limit three times in the last ten years and never below 93% (CEFAS & EA 2013); indicating the spawning stock of the River Frome, despite the numbers caught by recreational anglers, is healthy. In light of this, fishery management rules defining the actions of fishers to limit their impact seems to be working and other non-angling components may be affecting salmonid populations.

### *8.1.3 Assessment of current management regimes and recommendations*

One of the management objectives on the River Frome is to increase Atlantic salmon eggs deposited to numbers ( $2.09 \times 10^6$ ) even higher than the conservation limit (CEFAS & EA 2013). Whilst this is a management objective for the whole river, the efficacy of this to increase adult Atlantic salmon numbers needs to be evaluated at specific sites. The results of the investigation in chapter 4 looked at the impact of density dependence on the bodymass of individual fish highlights the potential for population enhancement regimes to fail under a set environmental conditions. As part

of GWCT Atlantic salmon research, an extensive PIT tagging program (circa. 10,000 – around 15-20% of the entire River Frome YoY Atlantic salmon population) of YoY Atlantic salmon is carried out annually (Beaumont et al. 2012). Tagging of YoY Atlantic salmon occurs across several sites on the River Frome in September with a subsequent smolt recapture happening the following May that records the number and the source (the site the parr were tagged in) of smolting fish, however, in recent years, the number of spring smolts has been declining (Beaumont et al. 2012). Overwinter survival of smolts has been highlighted as a potential reasons for reduced smolt numbers and this information gap currently is being address (Beaumont et al. 2012). Chapter 4 showed that there is a threshold YoY Atlantic salmon population density beyond which the number of ‘large’ fish will not increase and this is a possible reason that explains the disagreement with relatively high egg densities but low smolt numbers on the River Frome. The threshold weight in that investigation defined a ‘large’ fish above a proxy weight (see chapter 4) and a better understanding of where this threshold weight should be sought. This information can then be used in conjunction with site-specific conditions for site-specific management on the River Frome. Additionally, the current management objective of increased egg densities above the conservation target should not take priority with resources allocated to identifying the cause of the disparity.

Another study by the Game & Wildlife Conservation Trust investigating the impact of long-term (multi-year) pike removal on local brown trout population densities showed that though there was a decline in estimated population densities of all age cohorts, this difference was non-significant. The adaptive antipredator behaviours of prey fish is discussed and modelled in chapter 7, showing the potential for nonlethal predator-prey interactions to negatively impact fish growth rates. It can be postulated that a regime of pike removal would result in a population of faster growing trout (as non-feeding antipredator behaviours are ceased) and a slower growing

population if pike were present; predation pressure selects against faster growing and risk-taking behaviour (Biro et al. 2004). Whilst they may be slower growing, fish that live in the presence of predation pressure have greater and more refined antipredator behaviour (Brown et al. 2013) and thus higher survival rates (Mirza & Chivers 2000). Considering the difficulties in maintaining a long-term pike-free site and the potential ecological benefits of having a population of large pike (see discussion in chapter 7), a fishery may be more economically sustainable and have fish with higher survival adaptability if pike culling was not implemented. Fish have indeterminate growth and slower growing fish does not mean smaller fish, rather, it just means it takes slightly longer for them to grow big into angler-targeted, trophy specimens. Furthermore, if a fishery adopts an ecosystem-approach to its management, and the welfare of other fish species are also promoted; the total number of salmonids predated by pike should be low. For these reasons, it seems that a case needs to be made for, not against, a regime of pike removal.

The management of *Ranunculus spp.* to mitigate the risk of flooding will cause significant impacts on river hydrology, sedimentation rates and on invertebrate community (Gregg & Rose 1982, 1985; Madsen et al. 2001). It is assumed that this resulting change to the habitat and food availability will negatively impact salmonid populations but this was not predicted in model simulations (chapter 6). The results of those simulations show that the removal of the provision of overhead cover by the macrophyte plume structure and a consequent increase in fish stress is likely to be a mechanism for the recorded decrease in salmonid growth rates from field studies. To mitigate this impact, management might look towards designing cut regimes with different timing and/or the extent and amount of *Ranunculus spp.* removed to ensure that there is some overhead cover to maintain growth rates. Alternatively, management could look into replacing or providing artificial overhead cover that would not increase flood risk (e.g. a shaded net over the river would not affect flow but may provide sufficient cover to

keep fish unstressed). An added benefit of a shaded net is that it will also reduce the biomass of *Ranunculus spp.* stands under it and thus reduce flood risk (Dawson 1979). Analysis of the GWCT YoY Atlantic salmon PIT tagging data, identifying the source of the greatest numbers of smolting fish (i.e. the fish that survived the winter) could then be used to identify the habitat that is most conducive to producing fish that survive winter conditions.

Chapter 5 showed the potential impacts on salmonid growth rates by parasites that exert a high bioenergetic cost to salmonids. But these impacts are not just specific to parasites as the investigation method identified the impact routes and thus will apply to non-parasite diseases including from viral and bacterial infections. Known bacterial infections include *Aeromonas salmonicida* (Kingsbury 1961) and *Renibacterium salmoninarum* (Bruno 1986) and infectious salmon anaemia (Mjaaland et al. 1997) as an example of a viral infection that has been reported in Scotland (Murray et al. 2002). Current disease management in freshwater fisheries is heavily influenced by public perception and there is a knowledge gap that must be filled for evidence-based policy (Gozlan et al. 2013). The investigation in chapter 5 should be used to identify the threats to species of economic and ecological value so that management can prioritise research into i) understanding the risk of introduction into a population and ii) look to take preventative measures to prevent its introduction; this way management can adopt a proactive approach to the threat.

## 8.2 Future research

The findings and conclusions of chapters in this thesis are heavily reliant on the assumption that the salmonid IBM has been robustly validated. Whilst the tests undertaken to validate the model (and that these tests go beyond the standard ‘pattern-orientated modelling’ validation proposed by Grimm & Railsback (2005)) there are always additional methods that can be performed to further test the model.

One counter argument is that the predictions of the model across all chapters might result by chance and the model assumptions may actually be incorrect. Such a possibility could arise from the relative complexity and heavy parameter design aspect of the model; given the numerous interactions between parameters, it is a challenge to grasp the underlying process that create the population patterns (Grimm & Railsback 2005). However, this ‘lack’ of defined process pathways is also one of the IBM approach’s strengths: patterns at the population level arise from interactions of individuals and there is no explicit definition of how a population should respond to the defined (and perturbations to the) environment. IBMs model from ‘bottom-up’ and the vast majority of assumptions at the individual level in this model (e.g. fish behaviour and bioenergetics are derived from published studies (e.g. Elliott 1975a, 1975b and 1976 into salmonid bioenergetics and Hughes et al. 2003 on salmonid drift feeding behaviour). These studies were empirical in their approach and a greater confidence can be associated with them as compared to if assumptions of bioenergetics and feeding behaviour were made during this investigation. One method to test the design in how these submodels interact (i.e. the way this IBM has constructed them together) can be done by comparing results from two or more salmonid IBMs with different model designs. For example, the trout IBM, inSTREAM, designed by Railsback et al. (2009) could be parameterised with one of the datasets in this investigation and certain assumptions of both models could be tested. Even further validation can be

achieved by validating the model with more patterns that could be collected from additional small field or lab-based experiments. If the underlying assumption that the foragers in the IBM developed here behave, grow and move like real Atlantic salmon and brown trout, an assumption could be made that they should behave the same in artificial conditions (i.e. especially if experiments were performed in artificial streams that were designed to reflect the chalk stream habitat). The extra control afforded by a study in an artificial stream will also overcome certain weaknesses in field-based collections of environmental parameters in this investigation (e.g. estimates of drift densities and channel flow characteristics). The virtual environment in the model could be parameterised on these artificial conditions and salmonid behaviour and population patterns of real fish could be used to validate the model predictions in the same approach in chapter 3.

These proposed tests will act as additional model validation but the robustness of the tests currently employed in this thesis should be given due credit. The project design of collecting data from complimentary fieldwork allowed for the collection of specific environmental and population parameters to create the virtual environment and to initialise the starting population. Model predicted population patterns are directly compared with the patterns observed in real salmonids and this approach is utilised in Goss-Custard et al. (2010) and their validation of their coastal bird IBM with the slight difference that their IBM was built first and then validated by applying it to a dataset of environment and bird population parameters. It should be noted that whilst validation was explicitly described in chapter 3 and 6, the predicted population patterns made in chapter 4 and 7 can and should also be interpreted as additional patterns for validation (weak patterns but still acceptable under ‘pattern-orientated modelling’ validation approach, see Grimm & Railsback 2005). In chapter 4, the predictions of decreased mean population growth rates under increased population densities and increased mean population growth rates with increased habitat

area and drift densities agree with predicted patterns according to established theories on density dependence and competition.

Examples of potential specific improvements that would increase the utility and power of the model include: i) the inclusion of forager mortality, increased duration to include a whole year time frame and ii) the inclusion of specific stages in salmonid life cycles. The environmental conditions in winter months consist of increased discharge, increased turbidity, higher velocity and water depth (Berrie 1992) and these pose difficult conditions in which to collect environmental data and especially population data. However, it may be plausible to make assumptions about the environmental conditions and if metrics on salmonid populations could be obtained in the spring period the following year, a method of calibration either as shown in chapter 6 or by Approximate Bayesian Computation (Beaumont et al. 2002; Jabot et al. 2013) could be used to parameterise the winter period.

The lack of fish death in the current IBM is an area that needs to be improved. Individual mortality in the population would alter density-dependence effects that would ultimately influence population patterns and increase the utility of the model to investigate the effects environmental change or even parasite introduction might have on population evolution. However, as estimating deaths and consequently natural mortality is very difficult to record and quantify in field observations (Vetter 1988; Hewitt et al. 2007) and without appropriate patterns on which to parameterise, it was purposefully excluded. Despite its importance, estimating natural mortality in fish populations remains a challenge for all fishery models (Hewitt & Hoenig 2005) but several methods have been proposed (see Hewitt et al. 2007 and Pauly 1980). The Metabolic Theory of Ecology (MTE) is another possible method of incorporating mortality (Brown et al. 2004; Sibly et al. 2013) and opens up potential future collaboration between other science disciplines. Mortality could be incorporated in future model developments



using the emigration function in MORPH (Stillman 2008). Nonetheless the model without fish mortality was still validated in chapter 3.

Making the model simulate multi-year effects is a potentially useful development to increase its utility beyond fishery private, small-scale fishery management to become useful for long-term management at regional and national scales (e.g. inSTREAM by Railsback et al. 2009). The model already has the capacity to model the increase in the length of the simulated period (if the caveats described above about parameterising the environment during the winter period are first addressed) and the ability for fish to grow and mature into different age classes could be modelled. There may be great utility for the model to be used a conservation tool if virtual fish are modelled to reach an age of sexual maturity and begin breeding so that the virtual population can repopulate and sustain itself as real salmonid populations do. However, chalk streams are managed as fisheries and management objectives differ from conservation objectives with a greater focus on more, larger ‘trophy’ fish (Arlinghaus & Cooke 2009), which the model currently is able to predict. Furthermore, this development would have limited use in Atlantic salmon and sea trout conservation as given the anadromous nature of these fish, the IBM would be hard pressed to increase its environmental scope to include marine habitats and model fish interactions there; there is very little current understanding of causations driving observed fluctuations and variation in marine survival (Environment Agency 2004). Nonetheless, the potential benefits and increased utility afforded by modelling multi-year scenarios for non-anadromous brown trout populations should be considered in future model simulations.

### 8.3 Conclusion

In addition to the management recommendations provided in preceeding sections, the following general conclusions can also be made:-

- The MORPH IBM modelling platform is robust and adaptable to other environments and animal species. It has proven successful in modelling coastal bird responses and here I have adapted it to fish populations in a chalk stream environment. As aquatic systems and fish bioenergetics are more complex than birds in terrestrial systems (i.e. indeterminate, temperature-dependent growth and a 3-D environment), there is scope for the simplification of the salmonid IBM to become more accessible and user-friendly.
- This thesis has also shown the utility and appropriateness of IBM and MORPH to tackle theoretical and applied issues. Investigations into the effects of specific fishery management regimes (chapters 4, 6 & 7) tackled current conflicts and contributed to an evidence-based management approach. The IBM was also used to tackle the threats of parasites and disease on salmonid populations and prioritised threats theoretically but has real applications to current understandings of parasite risk (chapter 6).
- The investigations are examples of the model's robustness at tackling challenges that current habitat-association models cannot address. It shows the potential for the model to have real contribution to management decisions in the same manner as bird IBMs have informed the management of cockle fisheries and their impacts on bird populations with Natural England.

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